







# PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL  
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

JAMES G. MOORE and WAYNE U. AULT  
*Historic Littoral Cones in Hawaii*

R. D. WOOD  
*The Characeae of Fiji*

ARLAND HOTCHKISS  
*Chromosome Numbers in Characeae from the South Pacific*

P. B. TOMLINSON  
*Stomatal Structure in Pandanaceae*

SATYU YAMAGUTI  
*New Monogenetic Trematodes from Hawaiian Fishes, I*

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*Revision of the Genus Pandanus*  
*Part 17. Borneo, Cambodia, and Vietnam*  
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(Continued on inside back cover)

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# Historic Littoral Cones in Hawaii

JAMES G. MOORE AND WAYNE U. AULT<sup>1</sup>

**ABSTRACT:** Littoral cones are formed by steam explosions resulting when lava flows enter the sea. Of about 50 littoral cones on the shores of Mauna Loa and Kilauea on the island of Hawaii, three were formed in historic time: 1840, 1868, and 1919. Five new chemical analyses of the glassy ash of the cones and of the feeding lava show that there is no chemical interchange between molten lava and sea water during the brief period they are in contact. The littoral cone ash contains a lower  $\text{Fe}_2\text{O}_3 / (\text{Fe}_2\text{O}_3 + \text{FeO})$  ratio than does its feeding lava because drastic chilling reduces the amount of oxidation.

A large volume of lava entering the sea (probably more than 50 million cubic yards) is required to produce a littoral cone. All the historic littoral cones were fed by aa flows. The turbulent character of these flows and the included cooler, solid material allows ingress of sea water to the interior of the flow where it vaporizes and explodes. The cooler, more brittle lava of the aa flows tend to fragment and shatter more readily upon contact with water than does lava of pahoehoe flows.

**LITTORAL CONES** are common features on the shores of the younger volcanoes of Hawaii (Wentworth and Macdonald, 1953:28). These cinder cones do not mark the site of a primary volcanic vent but rather are produced by the violent steam explosions which result when some lava flows enter the sea. Upon such occasions the contact of molten lava with sea water produces great jets of steam hundreds of feet high. These blasts carry the chilled and shattered lava high into the air. If wind and topography permit, some of this material falls back on the land and builds up a cone. Most of the material falls into the sea and is removed by ocean currents.

Because of their location on the sea coast, littoral cones are very transient features and are rapidly removed by the sea; consequently they are found only on the youngest active volcanoes. On the shores of Kilauea and Mauna Loa on the island of Hawaii there are approximately 50 littoral cones. No cones are known on the other

three volcanoes (Mauna Kea, Kohala, and Huai-lalai) of which the island is composed, nor have any littoral cones been mapped on any of the other Hawaiian Islands.

In historic time, cones have been formed at only three localities (Fig. 1). These three cones are of particular interest because their age and conditions of formation are known and because the lava flows which fed them can be identified. The three historic littoral cone localities are: (1) Sand Hills, produced by the 1840 Kilauea flow; (2) Puu Hou, produced by the 1868 Mauna Loa flow; and (3) the cone produced by the 1919 Mauna Loa flow.

## 1840 Cones

The remnants of the littoral cones produced in 1840 are on the coast 5 miles northwest of Cape Kumukahi, the east cape of the island (Fig. 1). The largest remnant is called Sand Hill and has an altitude of 118 ft, as shown on the 1924 topographic sheet. Shortly after its formation it was more than 300 ft high, according to Coan (Brigham, 1909:52), but it has been largely removed by the erosive action of the sea.

<sup>1</sup> U.S. Geological Survey, Hawaiian Volcano Observatory, Hawaii, and Isotopes, Inc., Westwood, New Jersey. Manuscript received September 11, 1963.

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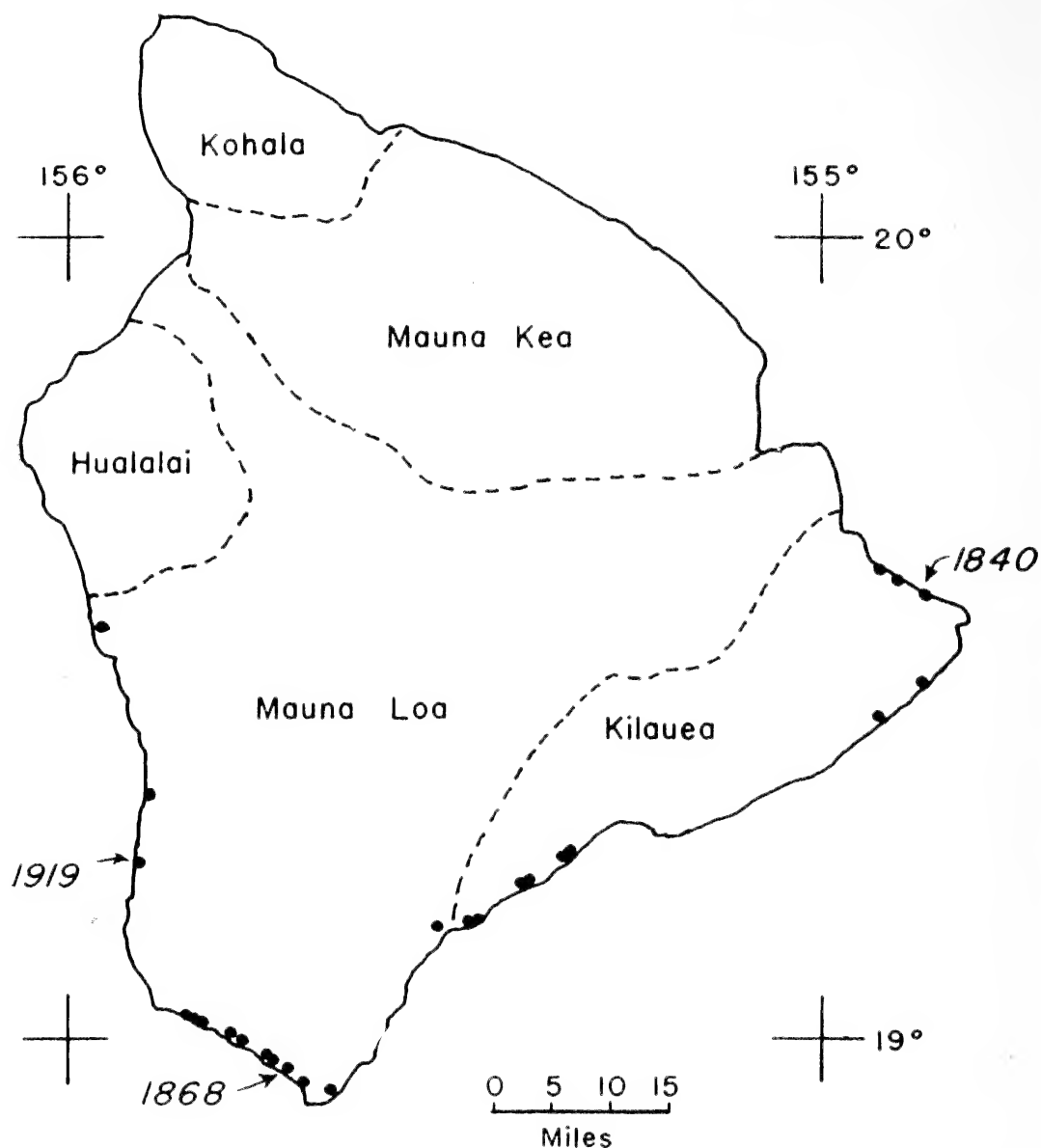


FIG. 1. Index map of the island of Hawaii, showing littoral cone localities (after Stearns and Macdonald, 1946) and year of formation of three historic littoral cones.

These cones were formed by a lava flow which broke out 7 miles inland at an altitude of 750 ft on the east rift zone of Kilauea on May 30, 1840, and continued flowing for a period of 26 days. The flow totaled approximately 281 million cubic yards, of which approximately 200 million flowed into the sea (Stearns and Macdonald, 1946:111).

The following vivid account by the Rev. Titus Coan (Brigham, 1909:52-54) describes the entry of the flow into the sea:

The flow . . . rolled down with resistless energy to the sea, where leaping a precipice of forty or fifty feet, it poured itself in one vast cataract of fire into the deep below, with loud detonations, fearful hissings, and a thousand unearthly and indescribable sounds. . . . The



atmosphere in all directions was filled with ashes, spray, gasses, etc.; while the burning lava, as it fell into the water was shattered into millions of minute particles, and, being thrown back into the air fell in showers of sand on all the surrounding country. The coast was extended into the sea for a quarter of a mile, and a pretty sand beach, and a new cape were formed. Three hills of scoriae and sand were also formed in the sea, the lowest about two hundred, and the highest about three hundred feet.

For three weeks this terrific river disgorged itself into the sea with little abatement. Multitudes of fish were killed, and the waters of the ocean were heated for twenty miles along the coast. The breadth of the stream, where it fell into the sea, is about half a mile, conforming itself, like a river, to the face of the country over which it flowed.

Brigham states further (1909:54) that:

The sand hills thrown up at this place were found to be one hundred and fifty, and two hundred and fifty feet high eight months after their formation, but since then the sea has removed the whole mass. Even in 1865 they were not a third of the measured height and nodules of olivine were abundant in the sands of the beaches at considerable distance.

Most of the remnants of the 1840 cones are composed of rather thin-bedded glassy ash and lapilli. In the wave-cut cliff facing the sea, the bedded ash lies on top of lava which is probably from the same eruption. A second lava flow overlies the bedded lapilli on the north side of the larger cone remnant. This lava flow has baked and oxidized the littoral cone ash a few inches below it. The upper flow represents continued movement of 1840 lava over the cone which was produced by the littoral explosions.

The littoral cone ash is crudely bedded, ranging from material 1 or 2 mm in size down to abundant silt-size dust. The 1840 flank lava was quite picritic, with approximately 20% olivine; consequently many of the ash particles are whole or fractured olivine crystals. Much of the cone is composed of beds of glassy ash about 5 cm thick, interbedded with layers about 1 cm thick of slightly coarser material. The coarser material is similar but contains a higher percentage of the larger chunks of glassy cinder, many from  $\frac{1}{2}$  to 1 cm in diameter, and some as much as 4 or 5 cm in diameter.

These beds can be traced for a hundred feet or more. The coarser beds may have been formed during the more violent phases of the steam explosions, or they may represent periods of

wind gusts which momentarily blew away the finer material.

### 1868 Cones

The littoral cones produced in 1868 are located on the coast 4 miles northwest of Ka Lae, the south cape of the island (Fig. 1). The main feeding flow passes between two cones; the one on the northwest is now 118 ft high, and the one on the southeast, called Puu Hou (new hill), is more than 240 ft high and about 1,500 ft in diameter at the base. A large part of Puu Hou has been eroded since its formation, and a substantial part has been removed since 1924, judging by photographs taken at that time by Stearns (Fig. 2).

The cones were formed by the lava flows from the Mauna Loa flank eruption at 2,500 ft altitude, which began April 7, 1868, and continued for 15 days. Of the 190 million cubic yards of lava erupted, about 100 million cubic yards flowed into the sea (Stearns and Macdonald, 1946:79).

There are no detailed descriptions by eyewitnesses of the actual formation of Puu Hou. However, Rev. Titus Coan, who visited the area in August, 5 months after the eruption, writes (Brigham, 1909:115):

Since three miles from the head the main stream went altogether over the precipice, and pursued its rapid course over the pahoehoe some seven miles to the sea which it reached in two hours. There it formed, as is usual when lava streams enter the sea, two cones of lava sand, or lava shattered into millions of particles by coming in contact with water while in an intensely heated state. There is no island there and there is nothing but what is common under similar circumstances. This stream is about half a mile wide, and it entered the sea some three-fourths of a mile from the big pali before spoken of. After running a day or two, in this channel, partial obstructions occurred, by cooling masses, when the shell of the stream was tapped some five miles from the sea, and a torrent of white-hot lava pushed out on the east side, running off to the great precipice and following its base in a breadth of half a mile down to the sea. . . .

In general the cinders composing Puu Hou are coarser than those of the other littoral cones studied. The cinders are crudely bedded, the differences between beds being mainly slight differences in size and sorting of the fragments.

Among the fine cinders and glassy ash are a



FIG. 2. Puu Hou, the littoral cone formed as the 1868 Mauna Loa flow entered the sea. Both photographs were taken from approximately the same point 38 years apart; above, June 14, 1924 (Stearns and Clark, 1930:7), below, by Moore and Ault, Feb. 1962.

great number of basalt bombs and spatter. Many of the bombs are subspherical, with concentric structure, and show evidence of having flattened when they hit. Most of them are covered with fine cinders which adhered to them when they struck the surface of the growing cone. The bombs are commonly 3–5 inches in diameter, but some more than 1 ft in diameter are present. Large masses of spatter as much as 8 inches in diameter drape over the cinders as high as the summit of the cones.

Puu Hou is notable in that it contains more bombs and spatter than the other cinder cones studied, indicating that a large amount of the material thrown into the air was still molten and was apparently not chilled and shattered. Very likely the steam explosions occurred near the base of a lava stream and threw molten material from the interior of the flow up onto the cone.

#### *1919 Cones*

The cone produced by the 1919 Mauna Loa flow is the smallest of the historic littoral cones. It is located on the southwest coast of the island, about 25 miles northwest of Ka Lae (Fig. 1). The cone is only about 50 ft above sea level and 15–20 ft above the general level on the landward side.

The 1919 Alikā flow which formed the cone broke out 11 miles east of the coast at an elevation of 7,500 ft on the southwest rift zone of Mauna Loa. The source vents opened about midnight, September 28–29, and the lava reached the sea at 4:30 AM, September 30. This aa lava stream continued to flow into the sea for 10 days. About 350 million cubic yards of lava were erupted, of which 200 million cubic yards flowed into the ocean (Stearns and Macdonald, 1946:79).

Many details of the contact of the lava with the sea were recorded by Thomas Jaggar of the Hawaiian Volcano Observatory (Jaggar, 1919: 133–134). When the lava poured into the sea, he wrote:

Noises were heard underwater of seething and of tapping concussions. The uprush of steam where the lava made contact with the sea carried up rock fragments and sand and built a black sand cone. The lava "rafts" or blocks of bench magma which rolled down the live channel, were seen to bob up, make surface steam,

and float out some distance from the shore without sinking at first, as though buoyed by the hot gas inflating them. Lightnings were seen in the steam column. There was much muddying of the water and fish were killed in considerable number. . . . For 50 or more feet out to sea from the base of the great column of vapor which was rising opposite the lava channel somewhere beyond, the water was dotted with small jets and sometimes a swirling "steam spout" or tornado effect, a foot or two in diameter, would rise from the water a few feet away from the main steam column and join the cloud above. Sometimes a shower of small rock fragments each two or three inches in diameter would be jetted up from a place in the water close to shore, each projectile followed by a tail of vapor, to heights 15 or 20 feet above the sea.

In describing the littoral cone as it appeared on October 23, a few weeks after the eruption, Jaggar stated (1919:151):

This cone, at the lower terminus of the channel was built by the steam explosions resulting from the incandescent torrent rushing into water, a crater being there formed, surrounded by a heap of black sand. This horse shoe heap was 75 feet high above sea level, and the front of it had broken down on the ocean side, revealing a section of bedded sands over a rock wall beneath. . . . The material was black and rather fine lava sand. . . . There were a few scattered small lava fragments on the surface of the sand. Everywhere the sand was coated with a thin film of crystalline white salt, common sea salt, to judge by the taste, and this made the cone white as seen at a distance.

The 1919 cone is composed of crudely bedded glassy ash and cinders. In the sea cliff this pyroclastic material is about 40 ft thick and extends from the crest of the cone almost to sea level, where it rests on top of a shattered and contorted lava flow. It is not known whether this flow is a 1919 lava flow or is older.

The east (landward side) of the cone is partly covered by a younger lobe of the 1919 flow. This lobe flowed on top and around the north side of the completed cone and reached the sea, forming a prominent peninsula containing a major channelway. In the sea cliff this younger lobe lies on top of the littoral cone ash and cinders and has baked them to a reddish color for a distance of 4 ft below its base. The younger lobe is not covered by cinders and apparently marks the last phase of the 1919 lava which flowed into the sea after the cone was formed.

The lower part of the clastic material of the

cone is relatively coarse. It is composed of rather large masses of spatter as well as angular blocks which are probably parts of the shattered solid top of the feeding aa flows. Many of these masses of spatter are 5-6 inches in diameter and 2 inches thick and are crudely disk-shaped. They occur in a matrix of finer cinders and glass sand. Higher in the cone the material is considerably finer grained and is composed predominantly of glass sand averaging less than a few millimeters in size.

The glass sand or ash from all three of the historic littoral cones appears very similar under the microscope. It is composed principally of angular fragments of fresh, light brown, trans-

parent glass containing abundant crystallites. In addition, 10 to 20 percent of the ash is composed of fragments of basalt and black, opaque glass. Small vesicles are common in both the transparent and opaque glass. They occupy 15 to 20 volume percent of the fragments and are generally 0.2 to 0.3 mm in diameter.

#### CHEMISTRY

Chemical analyses have been made of the glassy ash of each of the three historic littoral cones as well as of the lava flows which fed the cones (Table 1). Ash samples were collected 2 ft below the surface on the upper slopes of the littoral cones. Lava samples were collected from

TABLE 1

CHEMICAL ANALYSES OF HISTORIC LITTORAL CONE ASH AND ASSOCIATED LAVA FLOWS, HAWAII

	1	2	3	4	5	6	7	8	9	10
SiO <sub>2</sub>	48.86	48.43	— .43	51.03	50.58	— .45	51.89	51.83	— .06	— .31
Al <sub>2</sub> O <sub>3</sub>	11.46	10.70	— .76	13.20	12.63	— .57	13.90	13.95	+ .05	— .43
Fe <sub>2</sub> O <sub>3</sub>	2.13	1.15	— .98	3.26	1.65	— 1.61	3.24	1.75	— 1.49	— 1.36
FeO	9.09	10.08	+ .99	8.04	9.35	+ 1.31	7.88	9.17	+ 1.29	+ 1.20
MgO	14.13	16.29	+ 2.16	9.40	11.08	+ 1.68	7.21	7.05	— .16	+ 1.23
CaO	9.27	8.67	— .60	10.02	9.44	— .58	10.61	10.58	— .03	— .40
Na <sub>2</sub> O	1.84	1.71	— .13	2.22	2.01	— .21	2.25	2.31	+ .06	— .09
K <sub>2</sub> O	.36	.35	— .01	.42	.38	— .04	.36	.35	— .01	— .02
H <sub>2</sub> O+	.23	.22	— .01	.11	.33	+ .22	.06	.14	+ .08	+ .10
H <sub>2</sub> O—	.01	.00	— .01	.01	.13	+ .12	.01	.01	.00	+ .04
TiO <sub>2</sub>	2.14	2.00	— .14	2.13	1.94	— .19	2.10	2.11	+ .01	— .11
P <sub>2</sub> O <sub>5</sub>	.19	.18	— .01	.24	.21	— .03	.22	.22	.00	— .01
MnO	.17	.17	.00	.17	.17	.00	.18	.17	— .01	.00
CO <sub>2</sub>	.01	.00	— .01	....	.01	....	.01	.00	— .01	
Cl	.04	.02	— .02	....	.02	....	.01	.02	+ .01	
F	.03	.02	— .01	....	.03	....	.03	.02	— .01	
Total	99.96	99.99	+ .03	100.25	99.96	— .35	99.96	99.68	— .28	— .16

1. Olivine basalt from 1840 flow between 1840 littoral cone remnants at Sand Hill, Puna, Hawaii. D. F. Powers, U.S. Geological Survey, analyst.
2. Glassy basaltic sand 80 ft below summit of southern 1840 littoral cone remnant, Puna, Hawaii. D. F. Powers, U.S. Geological Survey, analyst.
3. Difference between 1 and 2.
4. Hypersthene basalt, lava of 1868, road near east edge of flow in Kahuku Ranch, Hawaii. J. H. Scoon, Univ. of Cambridge, analyst. Tilley and Scoon, 1961.
5. Glassy basalt sand, 100 ft below summit, Puu Hou (1868) littoral cone, Kau, Hawaii. D. F. Powers, U.S. Geological Survey, analyst.
6. Difference between 4 and 5.
7. Basalt from 1919 Alika flow 50 yards east of Alika littoral cone, Kona, Hawaii. D. F. Powers, U.S. Geological Survey, analyst.
8. Glassy basaltic sand from Alika (1919) littoral cone, Kona, Hawaii. D. F. Powers, U.S. Geological Survey, analyst.
9. Difference between 7 and 8.
10. Average of 3, 6, and 9.

near the surface of the aa flows; every effort was made to break out fresh rock and to avoid oxidized zones. A modern analysis is available (Tilley and Scoon, 1961) for one of the three flows (1868), and this is shown in Table 1. The purpose of these analyses was to investigate any chemical changes which occurred as the result of contact of incandescent molten lava with sea water.

In Table 1 the differences between the weight percent of the oxides of littoral cone ash and feeding lava are shown. These differences show virtually no chemical interchange between the lava and the sea water. Except for iron, MgO is the only oxide which shows an average difference of more than 1% between feeding lava and littoral cone ash in all three littoral cones. However, SiO<sub>2</sub> differs in a comparable, though smaller, degree in the opposite sense, suggesting that this difference in MgO is due to olivine control. Apparently the lava-flow material sampled had slightly less olivine than the littoral cone ash, and this difference in the amount of olivine is believed to be fortuitous.

Macdonald (1955:35) has had lava analyzed from above and below the tidal zone for two of the 1955 flows of Kilauea. These analyses also show virtually no interchange and no significant change in MgO or SiO<sub>2</sub> content.

All the analyses, however, do show a very interesting change in the oxidation state of the iron. The littoral cone ash is invariably higher in FeO and lower in Fe<sub>2</sub>O<sub>3</sub> than is the corresponding feeding lava flow, the littoral cone ash averaging about 1.2% more FeO and 1.4% less Fe<sub>2</sub>O<sub>3</sub> than the feeding flow. Likewise, the tidal zone 1955 lava is higher in FeO and lower in Fe<sub>2</sub>O<sub>3</sub> than is the subaerial part of the same flow (Macdonald, 1955:35), but the differences are smaller, averaging only about 0.5%. The reason for this difference, apparently, is that the rapid quenching of the water-chilled lava inhibits oxidation, whereas oxidation of iron proceeds in the subaerial part of the flow long after it has solidified, but while it is still hot. The smaller difference between tidal zone lava and its feeding flows, as compared with littoral cone ash and its feeding flows, suggests that the less drastic chilling of the tidal zone lava has allowed some oxidation to proceed in it, whereas that in the littoral cone ash was largely prevented.

Washington (1923:415–416) has pointed out that the more glassy forms of a lava flow contain a higher proportion of ferrous to ferric iron than do the more crystalline phases of the same flow. He has shown further that FeO is uniformly higher relative to Fe<sub>2</sub>O<sub>3</sub> in the pahoehoe form of lava flow than in the aa form; this difference is apparently due to the more glassy character of pahoehoe as compared with aa. Figure 3 is a compilation of modern analyses in which the  $\text{Fe}_2\text{O}_3/(\text{Fe}_2\text{O}_3 + \text{FeO})$  ratio is plotted for different kinds of flows, for pumice, and for littoral cone ash. These new data clearly support Washington's concept that iron in aa flows is more highly oxidized than that in pahoehoe flows. They also show that littoral cone ash and pumice from the Kilauea Iki eruption (1959) on the average are slightly less oxidized than the average pahoehoe flows.

All the feeding flows of the littoral cones are aa flows, yet the chilled littoral cone ash is in general less oxidized than pahoehoe lava and, with pumice, is some of the least oxidized of historic tholeiitic Hawaiian lava. Presumably, the characteristic high-oxidation state of the aa flows had not developed when the flow was in motion or when the littoral cones were built. Apparently the aa lava becomes highly oxidized rather late in the cooling history of the flow, probably after it solidifies, but before it is entirely cool. The greater thickness of the aa flows, as well as the insulating layer of rubble on the surface, would cause them to cool more slowly than pahoehoe flows, and hence they would be subject to oxidation for a longer period.

The state of oxidation of the iron in truly juvenile, unaltered Hawaiian tholeiitic lava is not known. However, the littoral cone glassy ash and basaltic pumice, both of which are drastically quenched, include the least oxidized of historic lava (Fig. 3) and may represent most closely the unoxidized lava.

#### MECHANISM OF FORMATION

The most important single factor in the formation of a littoral cone is that a flow of sufficient volume enters the sea. At most only a small amount, probably never more than 5%,



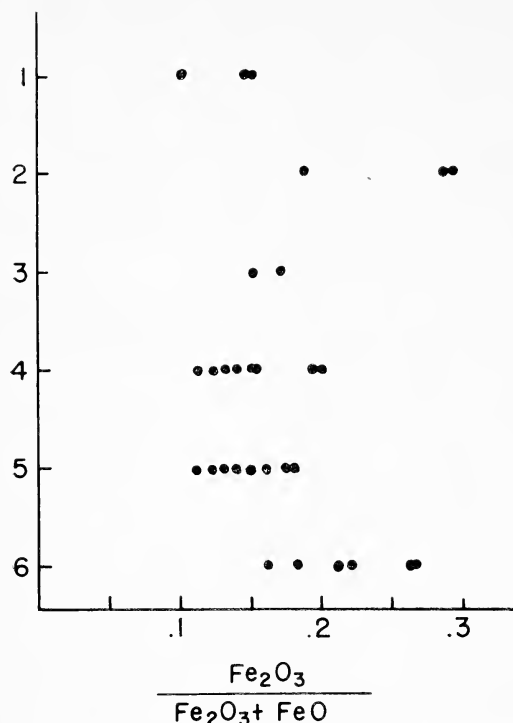


FIG. 3. Scatter diagram showing the  $\text{Fe}_2\text{O}_3 / (\text{Fe}_2\text{O}_3 + \text{FeO})$  ratio for different forms of historic basaltic lava from Kilauea and Mauna Loa.

1. Littoral cone glassy ash.
2. Aa flows feeding littoral cones.
3. 1955 lava collected in tidal zone.
4. Basaltic pumice.
5. Pahoehoe lava flows.
6. Aa lava flows.

of the lava is thrown into the air and back on land by the steam explosions. Hence, the volume of material which flows into the sea must be great. Judging from historic littoral cones, probably more than 50 million cubic yards of lava must enter the sea to produce a cone of appreciable size.

In Table 2 are tabulated the 12 historic lava flows which reached the ocean on the island of Hawaii. Of the nine which did not produce littoral cones, five poured too little lava into the sea. These five are the flows of 1750?, 1823, 1926, 1955, and 1960. Of these, the 1926, 1955, and 1960 flows produced observed littoral explosions and probably would have formed cones had the flows been more copious or more localized. The 1960 eruption poured a sizeable volume into the sea, but it was distributed along a 2-mile front.

All the littoral cones were fed by aa flows. Probably these lava flows are more likely to produce littoral explosions for two reasons: (1) The turbulent and fragmented character of the flow and the presence of much included, cooler, solid material, will allow ingress of sea water to the hot interior of the flow; this water will expand, form steam pressure upon heating, and explode. The pahoehoe flows, on the other hand, form an elastic crust on their surface but continue flowing within; hence the hot mobile interior is effectively sealed off from contact with the sea water. (2) The cooler, more brittle aa flows tend to fragment and shatter more readily upon contact with water than do the more fluid pahoehoe flows.

However, all large aa flows do not produce extensive littoral explosions and resultant cones. Aa lava flows differ greatly in the character of their flow. When the active feeding channel of the aa front is smooth and regular in its flow into the sea, littoral explosions and generation of steam appear to be inhibited. Macdonald (1954:166) pointed out that the unbroken liquid surface of the 1950 lava river which plunged into the sea prevented water from gaining access to the interior of the flow. When steam generation occurs only on the surface of the flow, the pressure required for the littoral explosions cannot build up. When the smooth surface of the flow where it entered the sea was disturbed, as by a floating raft of solid lava, a brief ash-making explosion occurred.

Undoubtedly other factors also contribute to the intensity of littoral explosions. In addition to the volume, rate, and character of the flow as it enters the sea, the character of the shore bottom is probably important. If the flow moves rapidly into deep water on a steep slope, the force of the explosions is lessened by the greater depth of overlying water.

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TABLE 2  
HISTORIC LAVA FLOWS ON THE ISLAND OF HAWAII THAT REACHED THE SEA

NUMBER	YEAR	VOLCANO	VOLUME IN MILLION CUBIC YARDS	
			Total	Submarine
1	1750?	Kilauea	19.5	?
2	1800-01	Hualalai	?	?
3	1823	Kilauea	15	3
4	1840	Kilauea	281	200*
5	1859	Mauna Loa	600	300
6	1868	Mauna Loa	190	100*
7	1887	Mauna Loa	300	200
8	1919	Mauna Loa	350	200*
9	1926	Mauna Loa	150	1.5
10	1950	Mauna Loa	600	100
11	1955	Kilauea	141	< 10
12	1960	Kilauea	156	10-30

\* Produced littoral cone.

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# The Characeae of Fiji<sup>1</sup>

R. D. Wood<sup>2</sup>

IN JUNE AND JULY, 1961, the writer made a concentrated search for Characeae in Fiji. Whereas these plants had previously been known only from outlying islands of Ovalau and Macuata-i-wai, they were found to be fairly common on the main islands as well and to include five species. The present systematic treatment is based upon the writer's collections and upon the few specimens available from other herbaria.

Earlier published records of Characeae report only two species from three collections. The first-known collection was made by the U. S. Exploring Expedition under Wilkes (1845:230 ff.) on Muthuate Island (= Macuata-i-wai), and it was described as *Nitella muthnatae* by T. F. Allen (1887:211). Later collections by Naumann in 1875 and Weber in 1882, both on Ovalau Is., were reported by Nordstedt (1888a:188) as *Chara australis* var. *vieillardii* f. *vitiensis*. These taxa are treated here as *Nitella pseudoflabelata* and *Chara corallina* (dioecious strain), respectively.

The Fiji Islands straddle the International Date Line (180° long.) at about 17° 30' S and lie approximately 1,300 miles south of the equator. They are one of a series of archipelagoes which lie in a stepwise chain extending eastward from Australia at intervals of approximately 800 miles. Samoa lies to the east and New Caledonia lies to the west. The geology and weather have been described by Freeman (1951) and Derrick (1957). Fiji includes some 300 separate islands, but the major portion (6,180 sq miles) of the total land surface (7,055 sq miles) consists of the two main islands of Viti Levu and Vanua Levu. The larger islands are of the continental type, and are generally mountainous. Lying as

they do in the southeast trade winds, the islands receive regular precipitation (ca. 120 inches/year at Suva) on the eastward, or windward, side but are fairly dry on the leeward side in the rain shadow of the mountains. On the dry, or lee, sides rainfall (40–60 inches/year) is largely restricted to the five wet months of December through April.

Available aquatic habitats are numerous and include rugged mountain streams, meandering rivers, waterfall pools, coastal lagoons and marshes, a high mountain lake (Tavenui), and man-made habitats including rice fields, canals, ditches, lily pools, and taro patches.

The Characeae, instead of being rare as seemed indicated by the sparse previous collections, occur widely throughout the islands visited by the writer. In fact, they were found in 19% of the habitats visited. They seemed to be especially frequent in the drier parts of the islands. The most frequently inhabited sites were the flooded rice fields and pools in fields or open woods. Such habitats supported Characeae in more than 50% of the cases. Somewhat less frequently occupied sites were lily ponds, canals, and ditch ponds. By contrast, Characeae were very rarely found in rivers or small streams, natural marshes or taro patches.

It was surprising to find three species of *Nitella* abundant beneath a dense cover of water lilies (pools on the plain below the Adi Cakobou School near Sawani), almost invariably absent from the coastal marshes with the large fern *Acrostichum aureum* L., and totally absent from the mountain lake. *A. aureum*, according to Merrill (1945:52), grows in areas occasionally swept by sea water; the salinity doubtless excludes the Characeae. The one lake, Crater Lake on Tavenui, was found by Koroiveibau in 1961 to have deeply stained water and to be largely covered with a [sedge ?] mat. Characeae were also absent from roadside ditches, frequently a fertile habitat in Australia.

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Collecting was done from June 5 to July 30, 1961; and, as described earlier (Wood, 1962*b*), herbarium specimens, formalin-preserved samples, and selected bits fixed in Carnoy's (3:1) solution for cytological analysis were prepared. The main excursions were by car and on Viti Levu included two circuits on the island, as well as short trips from Korovau to the Wainamala River, from Suva to Sawani, and from Sigatoka up the Sigatoka River; on Vanua Levu, from Labasa westward to Seaqaqa and Macuata, and from Dalana near Savusavu Point some 15 miles eastward along the southern coast; and on Ovalau, from Levuka southward around the end of the island to Bureta. On Macuata-i-wai (just off the north central coast of Vanua Levu), the group went on foot from the Chief's koro on the northeast tip of the island around the east shore and about one-fourth the way to the south end of the island.

The classification and nomenclature follow the writer's revision (MS) and approximate his prior report (1962*a*). Place names are spelled according to Fijian practice; the conventions as summarized by Capell (1957) are used with *b* for the sound of *mb*, *d* for *nd*, *g* for *ng* (as in singer), *c* for *th*, *q* for *ng-g* (as in finger). Certain of the more frequently cited and easily misinterpreted names are Bola (pronounced Mbola), Cakobou (Thakombau), Cakaudrove (Thakaundrove), Colo (Tholo), Cuvu (Thuvu), Galoa (Ngaloa), Labasa (Lambasa), Macuata (Mathuata), Nabukavesi (Nambukavesi), Nacobo (Nathombo), Nadi (Nandi), Nadona (Nandonia), Nadroga (Nandronga), Naibasiri (Naimbasiri), Seaqaqa (Seang-gang-ga), and Sigatoka (Singatoka). In addition, Nordstedt's (1888*a*:188) "Leruka" and "Oralau" are here revised to Levuka and Ovalau. Both had been followed by Zaneveld (1940:129). Also, T. F. Allen's (1887:211) Muthnate Island is corrected to Mathuata (as Macuata in Fijian conventions).

Herbarium abbreviations follow Lanjouw and Stafleu (1959) except for the writer's personal collection (RDW). Duplicates have been distributed to BA, BM, L, LE, MEL, SUVA, and US; and remaining duplicates will be distributed to other herbaria.

## ACKNOWLEDGMENTS

The writer wishes to thank Dr. J. Parham,<sup>3</sup> Dr. D. Hinkley, P. Thompson, K. York, and Atunasia Maidoga (Roko of Macuata) for arrangements in Fiji; and Dominiko Koroiveibau, Samarasam Pillay, Vakuru Waibuta, and Bernard Vunibobo for aid in the field. Dr. Kozo Imahori of Osaka, Japan, provided the illustrations; and Dr. A. T. Hotchkiss of Louisville, Kentucky, made the antheridial chromosome counts.

REVISED CLASSIFICATION OF CHARACEAE  
(Wood, 1962*a*)

The closest known occurrences of non-Fijian taxa are indicated in parentheses.

Division CHLOROPHYTA  
Class CHAROPHYCEAE  
Family CHARACEAE

## I. Tribe Chareae

## 1. Subtribe Charinae

1. Genus *Chara*

1. Subgen. *Chara* (Diplostephanae)—none (nearest: Australia, New Caledonia)

2. Subgen. *Charopsis* (Haplostephanae)

1. Sect. *Charopsis*

1. *C. corallina* Kl. ex Willd.

2. Sect. *Agardhia*

2. *C. fibrosa* Ag. ex Bruz.

2. Genus *Lamprothamnium*—none (nearest: New Caledonia; New Zealand)

3. Genus *Lychnothamnus*—none (nearest: Australia)

## 2. Subtribe Nitellopsinae

4. Genus *Nitellopsis*—none (nearest: Malaya)

## II. Tribe Nitelleae

5. Genus *Nitella*

1. Subgen. *Nitella* (Anarthrodactylae)

1. Sect. *Nitella*—none (nearest: Asia)

2. Sect. *Rajia*

<sup>3</sup> Son of B. E. V. Parham, earlier Senior Botanist, Suva, and recently director of the Department of Agriculture, Apia, Western Samoa.

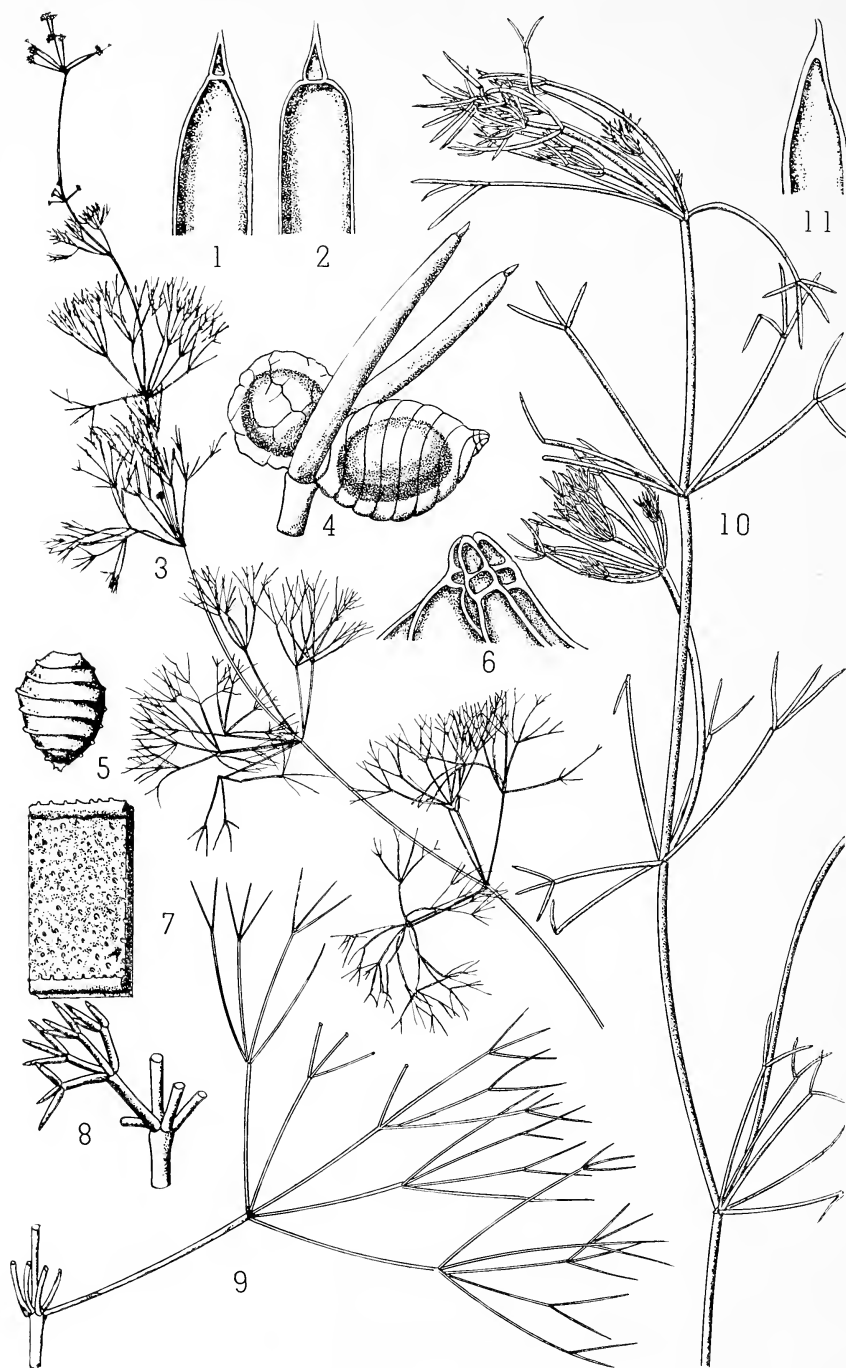


FIG. 1. Two common *Nitellas* of Fiji. 1-9, *Nitella pseudoflabellata*: 1-2, Apices of 2-celled dactyls,  $\times 90$ . 3, Habit,  $\times 1$ . 4, Terminal branchlet furcation with antheridium (at left) and oogonium,  $\times 44$ . 5, Oospore,  $\times 44$ . 6, Distal end of oogonium with coronula,  $\times 178$ . 7, Granular-papillate membrane in fossa between two adjacent ridges of oospore,  $\times 490$ . 8, Two-furcate, reduced branchlet,  $\times 16$ . 9, Sterile branchlet (2-) 3-furcate,  $\times 4$ . 10-11, *Nitella acuminata*: 10, Habit,  $\times 1$ . 11, Apex of 1-celled dactyls,  $\times 90$ . (1-9 From spec. k; 10-11 from spec. f.)



- 3. *N. acuminata* A. Br. ex Wallm.
- 3. Sect. *Knightria*—none (nearest: Africa)
- 4. Sect. *Brownia*—none (nearest: N. & S. America)
- 5. Sect. *Riddellia*—none (nearest: N. & S. America)
- 6. Sect. *Palia*—none (nearest: Japan; Australia)
- 2. Subgen. *Hyella* (Pluricellulatae, pp. [allantoid])—none (nearest: New Caledonia; New Zealand; Australia)
- 3. Subgen. *Tieffallenia* (Arthrodactylae)
  - 1. Sect. *Tieffallenia* (Mucronatae)
    - 4. *N. furcata* (Roxb. ex Bruz.) Ag.<sup>4</sup>
  - 2. Sect. *Gioallenia*
    - 5. *N. pseudoflabellata* A. Br.<sup>5</sup>
  - 3. Sect. *Decandollea*—none (nearest: New Caledonia; New Zealand)
  - 4. Sect. *Earthya*—none (nearest: Africa)
  - 5. Sect. *Muelleria*—none (nearest: Australia)
  - 6. Sect. *Vogania*—none (nearest: Australia)
  - 7. Sect. *Persoonia*—none (nearest: Australia; Japan; New Caledonia; New Zealand)
  - 8. Sect. *Migularia*—none (nearest: Australia)
- 6. Genus *Tolypella*
  - 1. Sect. *Tolypella*—none (nearest: Australia)
  - 2. Sect. *Rothia*—none (nearest: Asia)

KEY TO CHARACEAE OF FIJI

- 1a. Branchlets not furcate.....*Chara*
- 2a. Totally ecorticate.....1. *Chara corallina*<sup>6</sup>

<sup>4</sup> as *N. mucronata* by Wood (1962a:17).  
<sup>5</sup> includes *N. mutbnatae* T.F.A.  
<sup>6</sup> *C. braunii*, known from Hawaii and New Zealand, is monoecious with strongly developed stipulodes and bract-cells.  
<sup>7</sup> *C. zeylanica*, known to occur as near as New Caledonia and Hawaii, is diplostephanous (two tiers of stipulodes) and has branchlets more or less corticated but with the basal branchlet segment regularly ecorticate.

- 2b. Axes corticated.....2. *Chara fibrosa*<sup>7</sup>
- 1b. Branchlets (at least fertile ones) furcate.....*Nitella*
- 3a. Anarthrodactylous (dactyls 1-celled).....3. *Nitella acuminata*
- 3b. Arthrodactylous (dactyls 2-more-celled)
  - 4a. Brachydactylous (some of the dactyls tiny).....4. *Nitella furcata*
  - 4b. Macrodactylous (dactyls not tiny).....5. *Nitella pseudoflabellata*<sup>8</sup>

I. Tribe CHAREAE

1. *Chara* L.

2. Subgenus *Charopsis* (Kütz.) Leonh.

1. Section *Charopsis*

- 1. *Chara corallina* Kl. ex Willd., em. R.D.W.—*Chara corallina* Klein ex Willdenow (1805: 89); *C. australis* R. Brown (1810:346); em. Wood (1962a:12), em. Wood (1962a: 12).

Figs. 2, 3

REFERENCES FOR FIJI: *Chara australis* var. *vieillardii* f. *vitiensis* Nordst.: Nordstedt (1888a: 188; 1888b:8); and Zaneveld (1940:128); *C. corallina* var. *corallina*: Wood (1962a:12).

DESCRIPTION OF FIJI MATERIAL: *Plants* dioecious, 10–30 cm high, with dull finish when dry. *Axes* 500–980  $\mu$  in diameter, slender to moderately stout; internodes 2–8 cm long, 1–2 times as long as the branchlets; cortex none; nodes of axes commonly swollen and congested with a white material. *Stipulodes* in 1 tier, 2 per branchlet, 0–1 $\frac{3}{4}$  times as long as the axis diameter, slender, commonly up to 600  $\mu$  long and 60  $\mu$  wide and stiffly spreading; widely variable, and obscure or absent in some collections. *Branchlets, sterile*, 5–7 in a whorl, 1–3.5 (–6) cm long, undivided, spreading and fairly straight; segments 3, the end segment generally 2-celled with the end cell a conical mucro which is variable in length, commonly 350  $\mu$  long by 120  $\mu$  wide; *fertile*, same as sterile or reduced, where reduced may form into terminal or lateral heads (especially in  $\delta$ ). *Bract-cells* 0–4 at a node, commonly absent, where present  $\frac{3}{4}$ –1 $\frac{1}{4}$  times as

<sup>8</sup> *N. tenuissima*, reported from Palau, has a strongly reticulate oospore membrane and forms no heads or mucus.

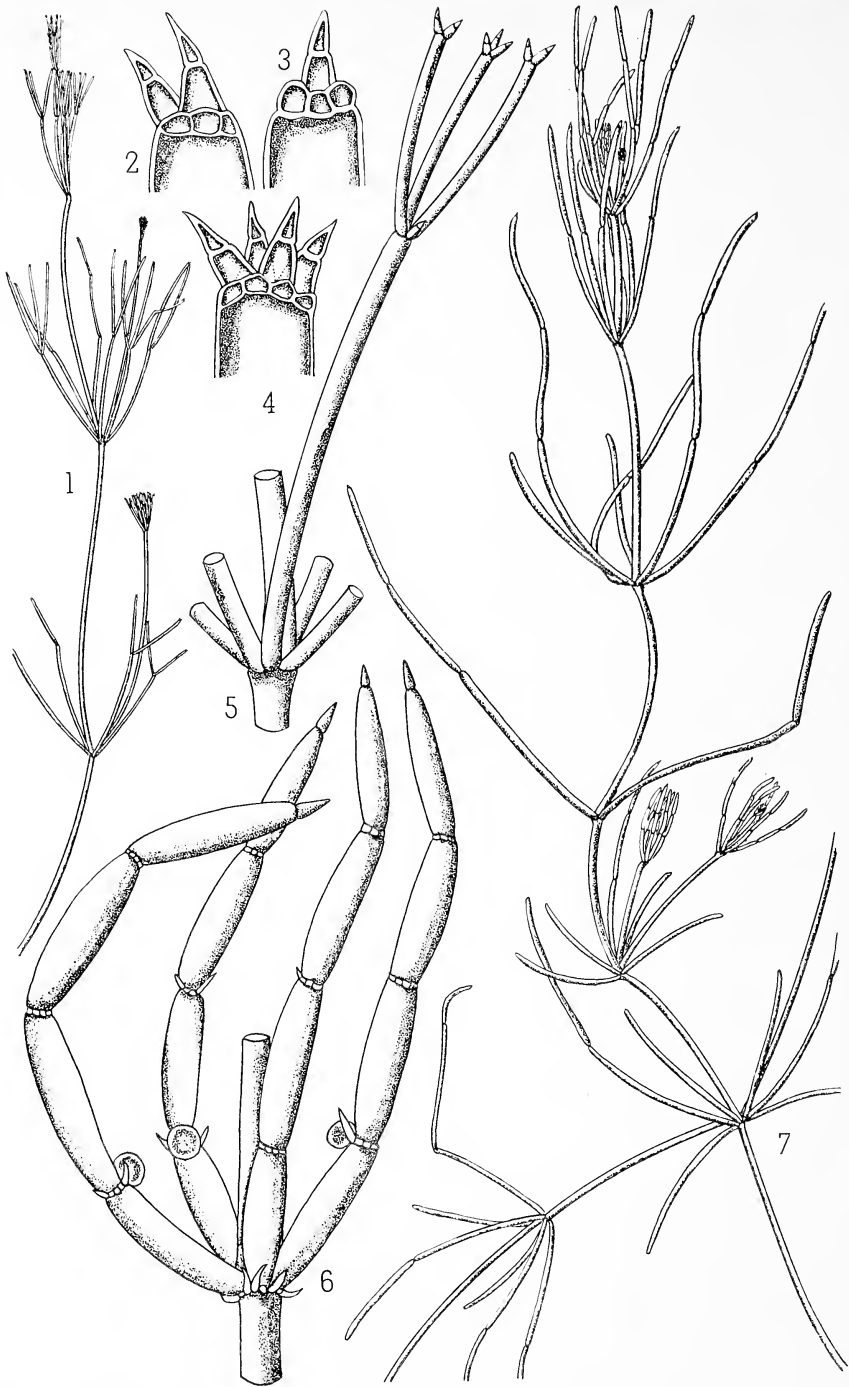


FIG. 2. A rare *Nitella* and a common *Chara* of Fiji. 1-5, *Nitella furcata*. 1, Habit,  $\times 1$ . 2-4, Apices of sterile branchlets showing ultimate furcation into 2-celled dactyls (there being variously 2, 1, and 4 dactyls shown) subtended by peripheral nodal cells; 2 and 3  $\times 130$ , 4  $\times 86$ . 5, Two-furcate sterile branchlet with a short 2-celled dactyl at the 1st furcation and abbreviated terminal dactyls,  $\times 12$ . 6-7, *Chara corallina* (dioecious strain, earlier *C. australis*). 6, Branchlet whorl of  $\delta$  thallus, showing well-developed stipulodes and the bract-cells at the lowest and 2nd (in center two branchlets) nodes,  $\times 10$ . 7, Habit of sterile thallus,  $\times 1$ . (1-5 From spec. a; 6-7 from spec. j.)

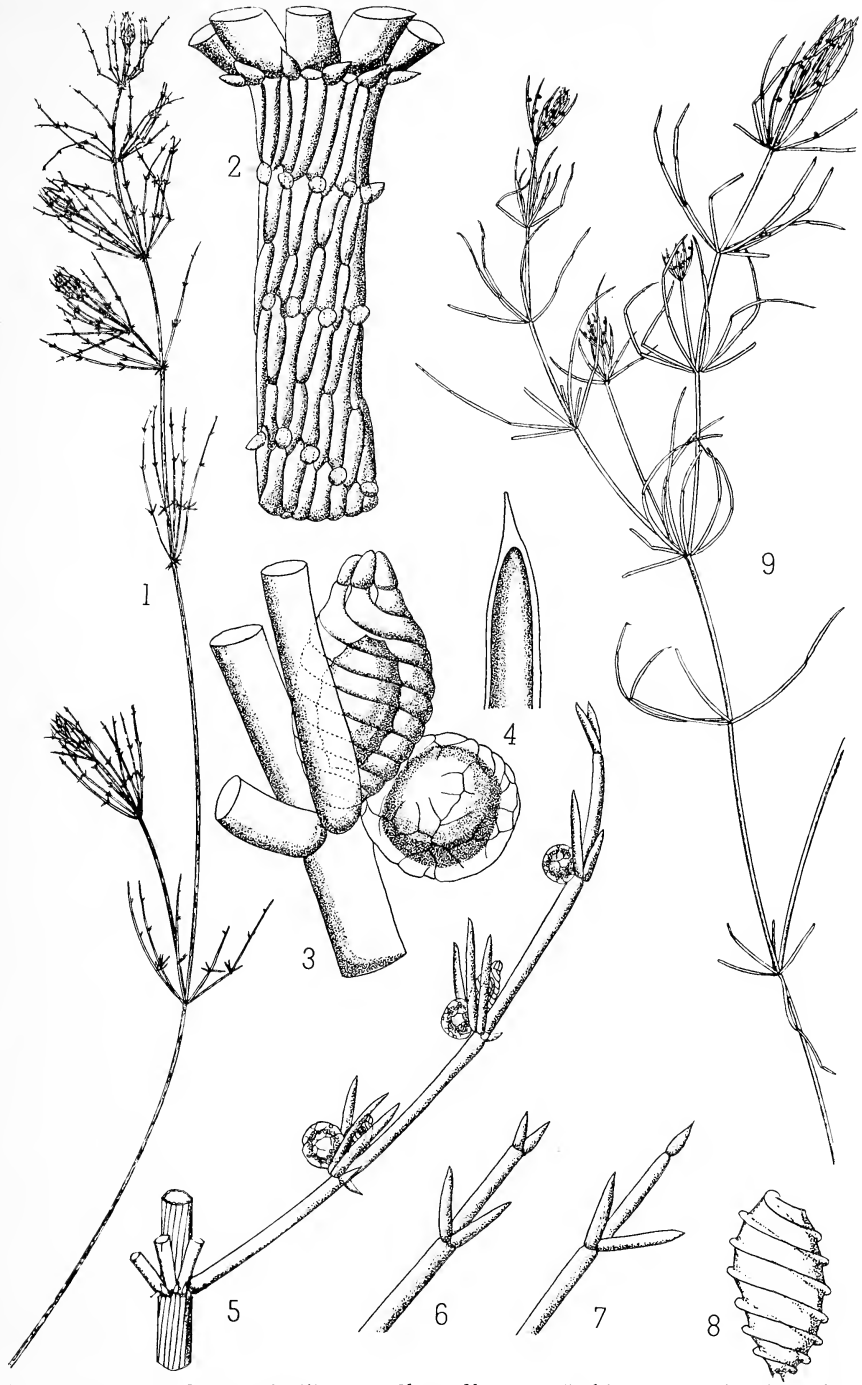


FIG. 3. The two common Charas of Fiji. 1-8, *Chara fibrosa*. 1, Habit,  $\times 1$ . 2, Portion of axis and node showing short alternating stipulodes (large ones have been lost) and the 2-corticated axis,  $\times 44$ . 3, Fertile branchlet node with oogonium above antheridium and two large bracteoles,  $\times 44$ . 4, Apex of bract-cell,  $\times 89$ . 5, Axial node and one branchlet with 5 segments and 3 fertile nodes, the two lowest having conjoined gametangia,  $\times 17$ . 6, Apex of branchlet showing bract-cells,  $\times 1$ . 7, Apex of branchlet with end cell apparently without node,  $\times 16$ . 8, Oospore with 7 broadly flanged striae and the basal spurs,  $\times 44$ . 9, *Chara coralina*, a  $\delta$  thallus with numerous antheridia,  $\times 1$ . (1-8 From spec. h; 9 from spec. m.)

long as the branchlet diameter, separated by two obvious peripheral nodal cells; where bract-cells are not developed, the peripheral nodal cells form a ring. *Bracteoles*, none noted. *Bractlet*, not noted. *Heads* uncommon, but antheridial branchlets are occasionally reduced forming loose heads 3–5 mm in diameter. *Gametangia* on separate plants, at 1–2 lowest branchlet nodes and occasionally 1 per branchlet on inside of whorl at base of branchlets; mature antheridia commonly on small whorls congested into heads. *Oogonia* (1–) 2–3 at the lowest 1–2 branchlet nodes, 780–1080  $\mu$  long (excluding coronula) by 610–680  $\mu$  wide; convolutions 6–7 (–8); coronula 100–105  $\mu$  high by 140–180  $\mu$  wide at base, 5-celled in 1 tier, the cells triangular. *Oospores* black, (560–) 600–660  $\mu$  long, 470–580  $\mu$  wide; striae of (5–) 6 broad ridges; fossa 105–130  $\mu$  across; membrane opaque and apparently smooth. *Antheridia* 2–3 at a node, (280–) 480–580  $\mu$  in diameter, generally borne on reduced branchlets but occasional at normal branchlet nodes; 8-scutate.

*C. corallina* is easily recognized in Fiji in the field by the crisp turgid nature and large size, and by having both undivided branchlets and totally uncorticated axes. *Nitella furcata*, although sometimes difficult to differentiate in the field in depauperate examples, is generally distinguishable by having forked branchlets and the tiny 2-celled, abbreviated dactyls. When the two species are mixed (e.g., spec. t), the two may appear to be one confusing species.

This is essentially the *C. australis* f. *vitiensis* of earlier writers. *C. australis* was distinguished from *C. corallina* by being dioecious; but the writer's investigations (MSS) indicated that in two otherwise indistinguishable "species" dioeciousness is a genetic state (half of the normal chromosome number) which may occur at random and is not a species distinction. Therefore, the monoecious *C. corallina* and dioecious *C. australis* were united (Wood, 1962a:12), and the oldest name, *C. corallina*, is employed. Specimens exhibiting the dioecious condition are here designated as "dioecious strains."

The Fiji specimens seem fairly unusual because of the small stature, slender structure, and occurrence of two rather than one stipulodes per

branchlet. They also appear to have small antheridia (480–580  $\mu$ ) for a dioecious strain (see Queensland, 800–1000  $\mu$ , and Tasmanian, 1250  $\mu$ , examples), and to have the axial nodes unusually swollen and congested with white material. It may prove to merit varietal status. The holotype of f. *vitiensis* was apparently destroyed in Berlin; and, as no duplicates have as yet been found, the writer suggests that specimen r (US) be accepted as the NEOTYPE.

The chromosome number of 14 is consistent with earlier reports of Macdonald and Hotchkiss (1956:277) who found 14 and 28, respectively, for dioecious and monoecious material from Australia. The second author's further unpublished counts of Australian "species" also appear to conform to this pattern.

Variations among collections were not great, but at two extremes are examples which seem to depend for their structure upon ecological conditions. One is small and slender with short branchlets, the axis less than 580  $\mu$  in diameter, the plants generally 12 (rarely 20) cm high, and the branchlets up to 2 cm long (see spec. e–i). The second is stouter, taller, and with longer branchlets, the axis 650–980  $\mu$  in diameter, the plants up to 30 cm high, and the branchlets commonly 3 (rarely to 6) cm long (spec. r). The latter appears to be a lush expression which develops in rich, shaded conditions such as in lily pools, while the former develops in exposed water of wet rice fields. In addition to these extremes, see spec. k which exhibits well-developed antheridial heads, and spec. f which has basal oogonia.

**HABITATS:** Rice fields, ponds, drainage ditch, pool by bridge, water lily pool, creek, river.

**DISTRIBUTION:** In Fiji, collected on Viti Levu (Nadroga, Naitasiri, Tailevu), Ovalau, and Vanua Levu (Macuata near Labasa, Natua, Macuata-i-wai, and Cakaudrove near Savusavu). *C. corallina* is restricted to the eastern hemisphere, where it is widely distributed in the tropics and extends into the temperate regions (especially of the southern hemisphere). It is reported from Africa, Mauritius, India, Ceylon, Burma, Thailand, Japan, Philippines, Indonesia, Australia (including Tasmania), New Caledonia, New

Zealand, and Fiji. Monoecious strains are known from Africa, Mauritius, Asia, and Australia, and the dioecious strains occur in Asia, Australia, and on the islands of the South Pacific.

SPECIMENS: OVALAU ISLAND—(a) *Nau-  
mann*. Nov. 1875. Levuka (as "Leruka") (B,  
destroyed, not seen; ref. Zaneveld, 1940:129, as  
f. *vitiensis*, HOLOTYPE);—(b) *Weber* [573 ?].  
June 1882. In the marshes near Bureta "Oralau"  
(B, destroyed, not seen; ref. Nordstedt, 1888a:  
188, 1888b:8, as No. 573 and var.  $\beta$  *vieillandi*,  
and Zaneveld, 1940:129, as f. *vitiensis*,  $\delta$ );  
VANUA LEVU: Cakaudrove: (c) *R. D. Wood*  
61-7-1-1. July 1, 1961. Abundant in 1-2 ft of  
fairly clear water, mud bottom, large pool ca.  
100 ft SE of Loa Road at culvert L 284 ca. 26  
miles E of Savusavu airstrip, Cakaudrove Pen-  
insula (CYT F 20, n = 14; slender, oogonia  $920$   
 $\times$   $640$   $\mu$ , convolutions 7, oospore black,  $660$   
 $\times$   $380$   $\mu$ , striae 6, fossa ca.  $130$   $\mu$  across, antheri-  
dia  $580$   $\mu$  in diam, 2-3 at a node, axis  $750$   $\mu$  in  
diam); Macuata: (d) *A. C. Smith* 6698. Nov.  
25-Dec. 8, 1947. In flowing water of Korovuli  
River, Seaqaqa Plateau [vicinity of Natua, alt  
100-200 m] (L, US, as *C. corallina*, det. F. K.  
Daily) (dioecious);—(e) *R. D. Wood and*  
*Vakuru Waibuta* 61-6-29-2. June 29, 1961.  
Abundant in ca. 6 inches of clear water, mud  
bottom, pool in dry ricefield W of Nakoroutari  
Road, ca. 2 miles S of Nakama Road turnoff, ca.  
5 miles S of Labasa ( $\delta$ , small and slender, axis  
 $550$ - $600$   $\mu$  in diam; mixed with *N. pseudofla-  
bellata*) ( $e^1$ ) [ibid. 61-6-29-1. See *C. fibrosa*,  
mixed with some *C. corallina* on which CYT 16,  
n = 14 was counted];—(f) ibid. 61-6-29-4.  
Ibid. (with some basal oogonia, slender with axis  
ca.  $590$   $\mu$  in diam);—(g) ibid. 61-6-29-5. Ibid.  
(formal. only);—(h) ibid. 61-6-29-6. Ibid.  
(CYT F 17, n = 14; slender, ca.  $500$   $\mu$  in diam);  
—(i) ibid. 61-6-29-7. Ibid. (heavily fertile  $\delta$ ,  
axis  $550$   $\mu$  in diam);—(j) ibid. 61-6-29-9.  
Sparse in ca. 1 ft of still water, sandy mud, small  
embayment on SE shore of Nakama River, just  
N of ford ca.  $\frac{1}{8}$  mile SW of Labasa (RDW  
1536, Fig. 2) (nodes swollen, nodes and stipu-  
lodes with white deposit, axes ca.  $700$   $\mu$  in  
diam);—(k) ibid. 61-6-29-10. Ibid. (axes ca.  
 $700$   $\mu$  in diam);—(l) ibid. 61-6-29-11. In ca.  
3 inches of dark water, mud bottom, long ditch

pool W of Nakama Road ca. 200 yards N of  
Nakama school ca. 3 miles SW of Labasa (axes  
ca.  $650$   $\mu$  in diam);—(m) ibid. 61-6-30-10.  
June 30, 1961. Abundant in ca. 1 ft of clear  
water, silty sandy-mud bottom, pool called "Na-  
lioniga" W of road ca. 1 mile past Seaqaqa Agric.  
Farm (RDW 1534, Fig. 3);—(n) ibid. 61-6-  
30-11. Ibid. (formal. only;  $\delta$  and  $\eta$ );—(o)  
ibid. 61-6-30-12A. Sparse in ca. 10 inches of  
clear water, ibid. (formal. only; oogonia  $560$ -  
 $930$   $\mu \times 380$ - $700$   $\mu$ , coronula  $105 \times 140$   $\mu$ ,  $\delta$   
 $480$   $\mu$  and on reduced branchlets);—(p) ibid.  
61-6-30-12C. Ibid. (formal. only; a few scraps  
mixed with *N. pseudoflabellata*); Macuata-i-  
wai [Mathuata Island]: (q) ibid. 61-6-30-1.  
June 30, 1961. Common at water's edge in ca.  
10 inches of water, sandy bottom, pool in creek  
at place known as "Vuniwesi" ca.  $\frac{1}{4}$  way around  
island to south from koro (formal. only; oogonia  
 $1000$   $\mu$  long, convolutions 7 (-8),  $\delta$  and  $\eta$ );  
VITI LEVU: Nadroga: (r) *R. D. Wood and*  
*Family*, 61-7-9-1. July 9, 1961. Common in ca.  
6 inches of clear water, silty mud bottom, N  
edge of pool with water lilies, Burns Point at E  
end of Sigatoka Bay (nodes with hard white  
deposit (negative for lime with dil.  $\text{HNO}_3$  and  
starch with IKI), stipulodes 2 per branchlet in  
a firm ring; axes  $750$   $\mu$  in diam, branchlets 6 cm  
long) (spec. in US suggested as NEOTYPE of f.  
*vitiensis*); Naitasiri: (s) *S. Pillay and A. Vua-  
lili*, Suva, 12498. July 12, 1961. Abundant,  
Sawani R., 1 chain below bridge, N shore [Wai-  
manu R. at Sawani ?] (axis  $650$   $\mu$  in diam);—  
(t) ibid., Suva 12499. Ibid. (mixed with speci-  
men labeled *N. furcata*); Tailvu: (u) *B. E. V.*  
*Parham* 742. Aug. 1, 1937. Forming large patches  
in shallow water, Wainimalo River, alt 700 ft  
(SUVA, as *Nitella*, det. R. D. Wood) [there is  
only a small region where the river touches Tai-  
levu, but the writer visited the area in July 1961  
and found no Characeae].

2. Section *Agardhia* R.D.W.

2. *Chara fibrosa* Ag. ex Bruz., em. R.D.W.—  
*Chara fibrosa* Agardh ex Bruzelius (1824:  
21); *C. flaccida* Braun (1849:296); *C. Ben-  
thamii* Braun (1867:799); *C. gymnopitys*  
var. *Benthamii* (A. Br.) J. Groves (1924:  
373) (orth. mut. to "Benthamii"); *C. fi-*

*brosa* subsp. *gymnopitys* (A. Br.) Zaneveld (1940:158); *C. fibrosa* subsp. *flaccida* (A. Br.) Zaneveld (1940:162); em. Wood (1962a:13).

Fig. 3

REFERENCES FOR FIJI: none.

DESCRIPTION OF FIJI MATERIAL: *Plants* monoecious, 10–20 (–35) cm high, occasionally incrustal. *Axes* moderately slender, ca. 300  $\mu$  in diameter; internodes 1–1½ times as long as the branchlets; cortex 2-corticated, occasionally slightly overlapping, aequistriate to slightly tylacanthous; spine cells sparse, tiny, conical, 20–80  $\mu$  high and ca. 80  $\mu$  wide. *Stipulodes* in 1 tier, 1–2 at each branchlet, generally elongate, 1–3 times longer than the axis diameter, cylindrical with acute tips; very deciduous and apparently replaced by short conical stipulodes. *Branchlets*, all similar and potentially fertile, 8–10 in a whorl, 1–2 (–2.5) cm long, segments (2–) 3 (rarely 4), end segment generally 2-celled with a reduced end cell. *Bract-cells* generally 3, verticillate, short, 1/10–½ as long as the branchlet diameter, commonly 150–500  $\mu$  long and ca. 100  $\mu$  wide (highly variable). *Bracteoles* 2, longer than the bract-cells, ½–1½ times oogonium in length. *Bractlet*, none. *Gametangia* conjoined at lowest 2 (rarely 3) branchlet nodes. *Oogonia* 1 at a node, ca. 700  $\mu$  long (excluding coronula) and ca. 450  $\mu$  wide; convolutions ca. 9; coronula conical, ca. 70  $\mu$  high and 300  $\mu$  wide. *Oospores* dark brown (slightly immature), ca. 450  $\mu$  long and ca. 250  $\mu$  wide; striae of 7–8 prominent ridges, possibly prolonged into short basal spines; fossa ca. (72–) 84  $\mu$  across; membrane smooth, brown. *Antheridia* 320–480  $\mu$  in diameter; 8-scutate.

This species is the only local charad with cortication. The longitudinal lines on the axis can just be seen by holding the plant up against the sunlight, and they can be easily made out with the aid of a hand lens. Another corticated species, *C. zeylanica*, occurs as near as New Caledonia and may turn up in Fiji. It could readily be distinguished by having two distinct rows of stipulodes, whereas there is only one row in *C. fibrosa*.

Although commonly treated as *C. gymnopitys*, the older name of *C. fibrosa* has priority, and

Zaneveld (1940:153) re-established this as the correct name. The present writer (1962a:13) included both *C. gymnopitys* and *C. benthamii* in the type variety of *C. fibrosa*.

The chromosome number of 28 agrees with Hotchkiss' unpublished data on Australian examples of *C. fibrosa*.

Variation in gross appearance is slight, but there are considerable differences in details. Some specimens exhibit only short, conical stipulodes (spec. i), while others have the elongate ones (spec. k). Between these two extremes are a number which have few to many elongated stipulodes (spec. h), but where they are missing the gap is filled with the short ones. It would appear that the long stipulodes abscise, perhaps at an early stage of development, and are replaced by the short ones. Where two stipulodes occur, they arise one at each side of each branchlet; but, where only one stipulode remains, it may appear to be alternately inserted. Other features to be noted are a spiny appearance due to large bract-cells (spec. a), smooth appearance when bract-cells are small (spec. h), and an appearance intermediate between these two (spec. j). None of the features seems consistent. The peculiar irregularity of the stipulodes, their large size, and the tendency for the number to vary from 1 to 2 per branchlet agree with these characteristics of the forms previously designated as *C. benthamii*.

HABITATS: Rice fields, ponds, pool by bridge, pool in ditch.

DISTRIBUTION: In Fiji, collected from Viti Levu (Tailevu near Sawani and Natovi; Nadroga near Sigatoka and Cuvu) and Vanua Levu (Macuata and Macuata-i-wai). *C. fibrosa* is widely distributed throughout the tropic and temperate world, Europe being the only temperate continent from which it is unknown. In the western Pacific, it is also reported from Japan, the Philippine Islands, Indonesia, Australia (including Tasmania), New Caledonia, New Zealand, and Guam.

SPECIMENS: VANUA LEVU: Macuata: (a) R. D. Wood and Vakuru Waibuta 61–6–29–1. June 29, 1961. In ca. 3 inches of clear water, mud bottom, pool in drained rice field W of Nakoroutari Road ca. 150 ft W of culvert marker

K 33, ca. 5 miles S of Labasa; mature ♀, 2-cort., slightly tylacanthous, stipulodes 1–2 per branchlet, oospore fossae 72–84  $\mu$  across, [contains traces of *C. corallina* on which CYT F 16 was counted]; Macuata-i-wai [Mathuata Island]: (b) *ibid.* 61–6–30–1. June 30, 1961. Common at water's edge, in ca. 10 inches of clear water, sandy bottom, pool in creek at place known as "Vuniwesi" in a valley ca.  $\frac{1}{4}$  way around island to S from koro at E end (some stipulodes  $1\frac{1}{2}$  times axis diam in length);—(c) *ibid.* 61–6–30–2. *Ibid.* (formal. only; mixed with *N. pseudoflabellata*);—(d) *ibid.* 61–6–30–3. *Ibid.* (formal. only; sparse, mixed with *N. pseudoflabellata*);—(e) *ibid.* 61–6–30–4. *Ibid.* (formal. only; mixed with *N. pseudoflabellata*);—(f) *ibid.* 61–6–30–6A. *Ibid.* (formal. only; mixed with *N. pseudoflabellata*); VITI LEVU: Nadroga: (g) W. Greenwood 104. Sept. 12, 1920. In water in drain side of rock cutting, Sigatoka (K, as *Chara* sp., annotated *C. flaccida* by J. Groves);—(h) R. D. Wood 61–6–9–1. June 9, 1961. In ca. 6 inches of fairly clear water, mud bottom, pond in marsh N of Queen's Road ca. 1 mile W of Sigatoka Hotel (RDW 1564, Fig. 3) (incrusted throughout, stipulodes deciduous, first long then short);—(i) *ibid.* 61–6–11–2. June 11, 1961. In ca. 12 inches of clear water, mud bottom, drained rice paddy E of Queen's Road ca. 14 miles N of Cuvu (unusual, bracteoles 4, 1–2  $\times$  oogonium length, 2 (–3)-cort., nearly aequistriate, stipulodes small);—(j) *ibid.* 61–6–11–3. In ca. 12 inches of clear water, drained rice paddy W of Queen's Road ca. 23 miles N of Cuvu (cortex 2-cort., somewhat overlapping);—(k) *ibid.* 61–6–11–4. *Ibid.*, but in 3 inches of water (large, 28 cm high, stipulodes largely lost and the few remaining ones are long); Tailavu: (l) *ibid.* 61–6–28–1. June 28, 1961. In ca. 6 inches of clear fresh water, black muck bottom, small pool in ditch W of Natovi-Korovou Road ca. 13 miles N of Korovou (CYT F 15,  $n = 28$ );—(m) *ibid.* 61–6–28–2. *Ibid.*

## II. Tribe NITELLEAE

### 2. *Nitella* Ag. em. A. Br.

1. Subgenus *Nitella* (= *Anarthrodactylae*)
2. Section *Rajia* R.D.W. (= *Acuminatae*)

3. *Nitella acuminata* A. Br. ex Wallm., em. R.D.W.—*Nitella acuminata* Braun ex Wallman (1853:35, and 1854:263) (including "*N. acuminata*" var. *Bellangeri* Braun, 1849: 292); em. Wood (1962a:16).

Figs. 1, 4

REFERENCES FOR FIJI: none.

DESCRIPTION OF FIJI MATERIAL: *Plants* monoecious, (5–) 15–20 (–35) cm high, moderately slender to stout, with or without a dendroid central stalk and with or without fertile heads. *Axes* moderately stout, 600–1200  $\mu$  in diameter; internodes 1–2 times longer than the branchlets, 1–7 cm long. *Branchlets*, fertile, 6–7 in a whorl, 1–4 (–5) cm long but sometimes reduced, 1-furcate into 2–3 secondaries (dactyls in this case); primaries  $\frac{2}{5}$ – $\frac{4}{5}$  of branchlet length; *sterile* similar to fertile, not reduced. *Dactyls*, fertile, 2 (–3), (1/10–)  $\frac{1}{5}$ – $\frac{3}{5}$  of branchlet length, 0.3–3 cm long, 1-celled, tapering to an elongate acute or acuminate tip; *sterile* similar to fertile, but not reduced. *Heads* uncommon, but upper whorls occasionally somewhat compacted into loose clusters 1–10 mm across; without mucus. *Gametangia* conjoined at branchlet nodes, but where reduced whorls occur the gametangia are nearly completely restricted to these heads; generally 1 antheridium and 1–2 (–3) lateral oogonia at a node. *Oogonia* 1–2 (–3) at a node, 350–390  $\mu$  long (excluding coronula) by 295–320  $\mu$  wide; convolutions 8–9; coronula (28–) 30–35  $\mu$  high and 42–50 (–64)  $\mu$  wide, persistent, upper cells slightly longer than lower. *Oospores* dark brown, 248–280  $\mu$  long and (210–) 225–240  $\mu$  wide; striae of 5–6 (–7) flanged ridges; fossa regular and 40–50  $\mu$  across or variable and 37–50  $\mu$  across; membrane pale brown, smooth or loosely tuberculate with 15–18 (–30) figures across fossa, 1–3 diameters apart (spec. a). *Antheridia* 224–280  $\mu$  in diameter; 8-scutate.

This is the only Fijian charad which is ecorticated and which has routinely 1-furcate branchlets. *N. furcata*, which usually has branchlets 2-more furcate, may appear 1-furcate at times and resemble *N. acuminata*; but a close examination will reveal small terminal, 2-celled dactyls, whereas the entire dactyl is 1-celled in *N. acuminata*.

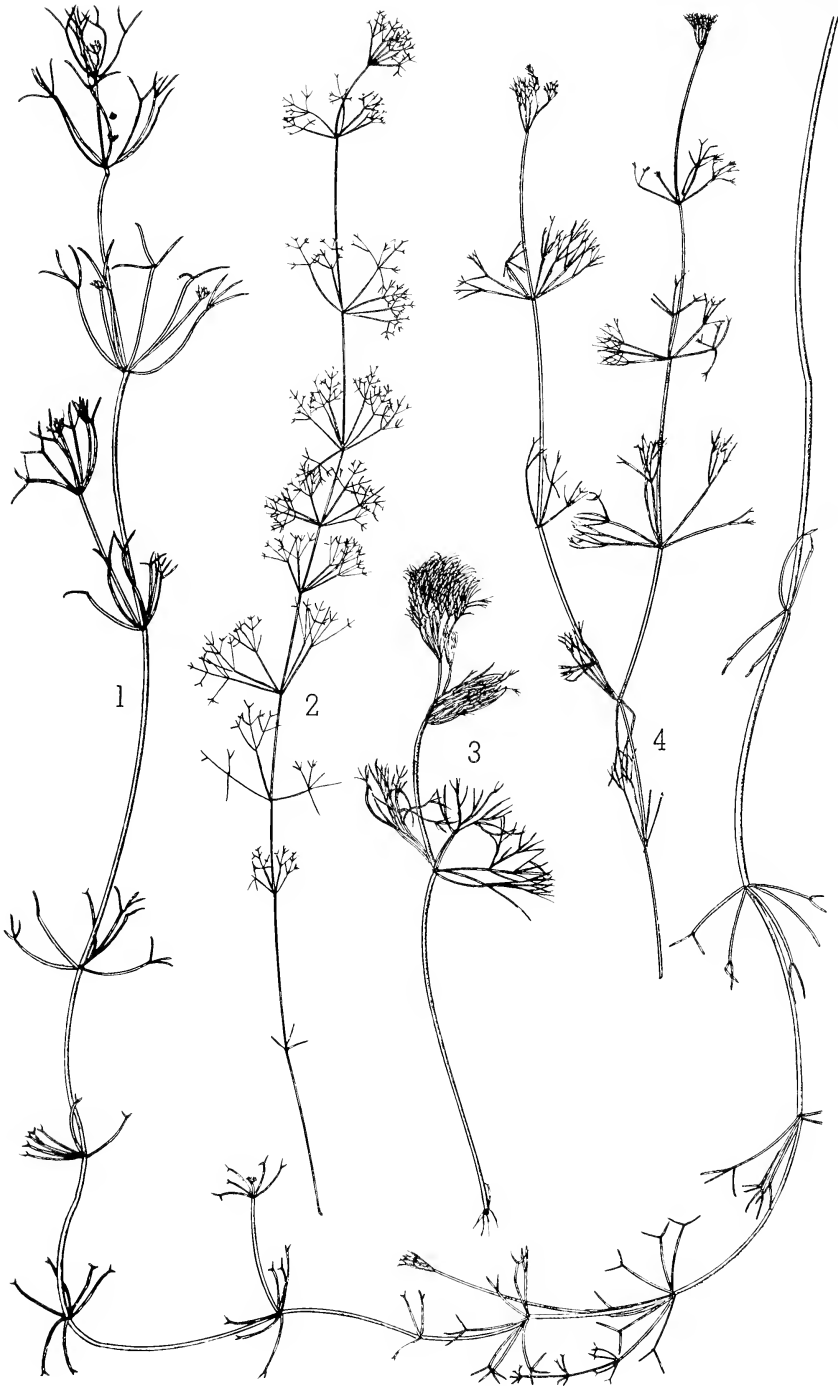


FIG. 4. Variations in *Nitellas* of Fiji. 1, *Nitella acuminata*, an elongate, lax specimen,  $\times 1$ . 2-4, *Nitella pseudoflabellata*. 2, Bushy form,  $\times 3$ . 3, Diffuse form,  $\times 1$ . 4, Mathuete form,  $\times 1$  (= *N. muhnatae* T.F.A.). (1 From spec. a; 2 from spec. af; 3 from spec. a; 4 from spec. p.)



The type variety, var. *acuminata*, is here broadened to include both the early sense, var. *Belangeri* Braun (1849:292), and that of the more diffuse forms, var. *diffusa* R.D.W. (Wood, 1962a:16).

The chromosome number of 18 agrees with Hotchkiss' (1958:15) earlier findings for North American material.

Variations are relatively minor and intergrade into one another; however, one extreme predominates in rice paddies and the other in pools. They appear to be ecologically induced fluctuations. One extreme is dendroid with an elongated lower axial internode which resembles a stalk and gives the plant a treelike habit. The plants also tend to be stouter throughout and to form distinctive heads (spec. d, f, g, j). The lax extreme has fairly uniform whorls evenly distributed along the axis, the plants tending to be more slender and not to form heads (spec. a, b, h). In addition to the above variations, it should be noted that some specimens exhibit unusual tuberculate rather than smooth oospore membranes. Otherwise they agree with *N. acuminata* (spec. d, f, h), and are not here separated on the membrane feature alone. Hotchkiss (in press) noted no differences in the chromosomes of these variants.

**HABITATS:** Rice fields, pools by bridge, pool by waterfall, lily pool, beach pool, creek, river. It apparently tolerates some salinity, as it occurred (spec. h) in a marsh which also had *Acrostichum aureum* L. The latter prefers "shallow brackish swamps" (Merrill, 1945:52). The apparent tolerance of *N. acuminata* to some trace of salt water in Fiji agrees with the observation of Wood and Muenscher (1956:11), who reported it from tidal mud flats of the Hudson River, New York.

**DISTRIBUTION:** In Fiji, collected only on Viti Levu (Naitasiri near Sawani; and Serua near Galoa and Navua). *N. acuminata* is widespread throughout the world, and absent from only one temperate continent, Europe. It is commonly reported from islands, and in the Pacific is known from Indonesia, the Philippine Islands, Formosa, and Japan.

**SPECIMENS:** VITI LEVU: Naitasiri: (a) *R. D.*

*Wood and S. Pillay* 61-6-26-2. June 26, 1961. In ca. 12 inches of fairly turbid water, mud bottom, amid water lilies in the [more] western of the two large lily ponds on the plain below the Adi Cakobou School, Sawani, ca. 18 miles N of Suva (RDW 1551, Fig. 4);—(b) *ibid.* 61-6-26-3. *Ibid.* (CYT F 14,  $n = 18$ ; primary rays 2-3 times dactyls in length); Serua: (c) *R. D. Wood* 61-6-8-1. June 8, 1961. In ca. 2 inches of clear water, muck bottom, old rice paddy ca. 6 miles E of Galoa, ca. 32 miles E of Korolevu Hotel (small fertile heads);—(d) *ibid.* 61-6-8-2. *Ibid.*;—(e) *ibid.* 61-6-25-1. June 25, 1961. In 3-4 inches of clear water, mud bottom, wet field N of road, ca.  $\frac{1}{4}$  miles N of Navua Hotel, ca. 28 miles W of Suva (CYT F 10,  $n = 18$ ; with some short dactyls 2-3 mm long);—(f) *ibid.* 61-6-25-2. In ca. 2 inches of clear water, mud bottom, rice paddy N of road, ca.  $1\frac{1}{2}$  miles W of Naitonitoni, ca. 29 miles W of Suva (RDW 1558; Fig. 1) (with some reduced dactyls and some small whorls);—(g) *ibid.* 61-6-25-3. In ca. 1 inch of clear water, mud bottom, tips of the *Nitella* projecting ca. 1 inch above water surface [water receding], rice paddy S of road, ca. 1 mile W of Naitonitoni, ca. 30 miles W of Suva;—(h) *ibid.* 61-6-25-5. In ca. 8 inches of clear fresh water, fairly firm mud bottom, pool ca. 50 ft behind beach, ca. 500 yards S of jetty at end of road, Naitonitoni, ca. 31 miles W of Suva; some *Acrostichum* in the adjacent marsh (mature ♀);—(i) *ibid.* 61-6-25-6. *Ibid.* (formal. only, mixed with and labelled *N. pseudolabellata*);—(j) *ibid.* 61-6-25-9. In 2-4 inches of fairly clear water, mud bottom, rice paddy N of Queen's Road 1 mile E of "Coronation Triangle" at Navua, ca. 26 miles W of Suva.

## 2. Subgenus *Tieffallenia* R.D.W.

(= Arthrodactylae, pro parte)

### 1. Section *Tieffallenia* (= Mucronatae)

4. *Nitella furcata* (Roxb. ex Bruz.) Ag., em. R.D.W.—*Chara furcata* Roxburgh ex Bruzelius (1824:22); *Nitella furcata* (Roxb. ex Bruz.) Agardh (1824:124); em. Wood (1962a:17).

var. *sieberi* (A. Br.) R.D.W.—*Chara mucronata* [var.] *Sieberi* Braun (1835:52); *Nitella polyglochin* var. *microcarpa* (A. Br.) T. F. Allen (1871:9); *N. microcarpa* var. *microglochin* (A. Br.) Zaneveld (1940:103); *N. mucronata* subsp. *furcata* var. *microcarpa* (A. Br.) Wood (1962a:18); *N. furcata* var. *sieberi* (A. Br.) Wood (1963:227).

## Fig. 2

REFERENCES FOR FIJI: none.

DESCRIPTION OF FIJI MATERIAL: *Plants* monocious, 15–30 (–more ?) cm high, varying considerably in habit from diffuse to strict; specimens depauperate. *Axes* moderately stout, 400–480  $\mu$  in diameter; internodes 1–4 times as long as the branchlets. *Branchlets*, fertile (not known, but probably not distinctive); *sterile* (5–) 6–8 in a whorl, 0.5–3 cm long, spreading at 40–60° angle from axis, irregularly (1–) 2 (–3)–furcate into (2–) 3 (–5) secondaries, and where present also into 1–3 tertiaries; primaries  $\frac{1}{2}$ – $\frac{2}{3}$  (–most) of total branchlet length, secondaries tiny in some cases or up to  $\frac{1}{4}$  of branchlet length. *Dactyls*, *sterile*, 2–3, generally reduced and tiny, 2-celled, penultimate cell rounded distally and wider than base of end cell; dactyls occasionally not reduced. *Heads* (not known, probably not developed). *Gametangia* absent (see Wood, 1963, for details from comparable Samoan material). (See Zaneveld, 1940:88, and Imahori, 1954: 105 and pl. XXIV, for descriptions of *N. furcata* (sens. strict.)).

This species is readily recognizable in Fiji as the only ecorticated charad which appears coarse and which has branchlets 2–more times furcate. Further, it has tiny 2-celled abbreviated dactyls. These are visible under a hand lens (see *C. corallina*).

As recently noted by the author (Wood, 1963), the names *N. furcata* and var. *sieberi* have priority and thus replace *N. mucronata* and var. *microcarpa* he had listed (1962a:17).

Unfortunately, no useful cytological material of this species was found in Fiji; but suitable stages were obtained in Western Samoa of a strain similar in all observable respects. The chromosome count of 18 (Wood, 1963:228) was obtained, which agrees with Gillet's (1959: 231) report of 18 in European *N. mucronata*

(= *N. furcata* subsp. *mucronata* in the present writer's revision).

Variations among the specimens were considerable, there being two extremes; but unfortunately no well-developed fertile material was obtained of either variant. A lax example has long branchlets up to 3 cm in length, and superficially resembles a lax *N. flexilis* in habit (spec. a). The other extreme is strict, has short branchlets up to 1 cm long, is dark gray green, and is long and slender in habit (spec. b). The lax variant occurred in a waterfall pool, and the strict material occurred in a river.

HABITATS: Pool below waterfall, in river.

DISTRIBUTION: In Fiji, collected only on Viti Levu (Naitasiri near Sawani). *N. furcata*, in the broad sense used here, is distributed throughout the world, and is known from the western Pacific in Indonesia, New Guinea, Australia (Queensland), the Philippine Islands, and Japan. The writer also found it in Western Samoa, but not in New Caledonia.

SPECIMENS: VITI LEVU: Naitasiri: (a) *R. D. Wood and S. Pillay* 61–6–26–4. June 26, 1961. In ca. 4 inches of rather turbid water, mud bottom, small pool on plain below Adi Cakobou School, ca.  $\frac{1}{3}$  way from lily pools to bridge, Sawani, ca. 18 miles N of Suva (RDW 1549, Fig. 2);—(b) *S. Pillay and A. Vuabili*, Suva 12499. July 12, 1961. Abundant in Sawani River [Waimanu R. at Sawani?], 1 chain below bridge (a confusing mixture of glossy specimens of *N. furcata* and dull specimens of *C. corallina*, at first thought by the writer to be *Nitellopsis* because the furcations of the *Nitella* resemble the long bract-cells of *Nitellopsis*);—(c) *ibid.*, Suva 12500. Abundant in Sawani River [Waimanu R. at Sawani?], below bridge on N side.

## 2. Section *Gioallenia* R.D.W.

5. *Nitella pseudoflabellata* A. Br. in A. Br. & Nordst., em. R.D.W.—*Nitella pseudoflabellata* Braun in Braun and Nordstedt (1882:54); em. Wood (1962a:19).

Figs. 1, 4, 5

REFERENCES FOR FIJI: *Nitella muthnatae* T.F.A.: T. F. Allen (1887:211), Zaneveld (1940:72), Wood (1952:352, nom. tant.), Wood and Imahori (1959:178); *N. gracilis* subsp. *leptosoma* var. *mathuatae* (T.F.A.) Wood

(1962a:20) (orth. mut.).—"nom. ined., '*N. Gibbsiae*' J. Gr. (herb. K)."

**DESCRIPTION OF FIJI MATERIAL:** *Plants* monoecious, (4-) 9-18 cm high, moderate in size, slender, light to dark green. *Axes* slender, (170-) 250 (-465) (570)\*  $\mu$  in diameter; internodes (1½-) 1-2 times as long as the branchlets, 1-4 cm long. *Branchlets*, *fertile*, (6-)\* 7-8 in a whorl, of normal size or reduced (0.6-1.2 cm long), (1-) 2-3 (-4)-furcate into (4-) 5-6 (-8) secondaries one of which is generally central and similar to the laterals, (3-) 4-5 tertiaries and (3-) 4-5 quaternaries; primaries ⅔-¾ of the total branchlet length; *sterile* similar to unreduced fertile branchlets. *Dactyls*, *fertile* and *sterile* similar, 3-4, 2-celled, (600-) 800-2000  $\mu$  long, (50-) 120  $\mu$  wide, basal cell tapering sharply to base of end cell or occasionally rounded distally, end cell conical and acute, 50-110  $\mu$  long, 30-35  $\mu$  wide, occasionally somewhat mucronate. *Heads* not well formed, but young (uppermost 1-2 internodes) fertile axes commonly elongate while their branchlets are still immature giving the appearance of terminal or lateral inflorescences, rarely compact and headlike. *Gametangia* conjoined at (1st-) 2nd (-3d) lower branchlet nodes, generally absent from lowest; protandrous, antheridia early deciduous. *Oogonia* 1 (-2) at a node, (360-380-)\* 420-495  $\mu$  long (excluding coronula) and (270-)\* 340-355  $\mu$  wide; convolutions 8-9 (-10), the cells unwinding slightly at maturity beneath the coronula; coronula (20-) 45-50  $\mu$  high and (20-) 35-50 (-56)\*  $\mu$  wide, upper cells 1½-2 (-3) times longer than the lowers. *Oospores* dull brown (slightly immature), (265-)\* 315-340  $\mu$  long, 230-245 (-255)  $\mu$  wide, 190  $\mu$  thick; striae of 5-7 (-8) slightly flanged ridges; fossa 42-52  $\mu$  across; membrane granular papillate, possibly appearing somewhat reticulate when pressed under a coverslip, 10-12 (-16) papillae across fossa, 2-3 diameters apart and ca. 2  $\mu$  high. *Antheridia* 1 at a node, 170-258 (-270)\*  $\mu$  in diameter, slightly wider than high, apparently 8-scutate.

\* Wood (in press).

This species is easily recognized in Fiji because of the delicate structure and tendency for repeatedly divided branchlets. Extreme examples which are more stout and have branchlets only 1-2-furcate can be checked under the microscope for the 2-celled dactyls.

The identity of the Fijian *Nitella* had been a matter of concern to the writer for some time. The existence of an endemic on an isolated mid-ocean island, apparently unrelated to species of adjacent continents, seemed remarkable. The present collections include complete sexual material and permit identification as *N. pseudoflabellata*. There is wide variation among the Fiji specimens, and the original type of *N. mathuatae* represents but one expression—a stout form with 1-2-furcate branchlets and occasional inflorescence-like apices. Based on original collections alone, Zaneveld (1940:72) had thought it might be *N. bipartita*, and the writer (1962a:20) had referred it to *N. gracilis* var. *leptosoma*.

The chromosome number of 18 differs from the only known prior reports of 24 from Japan (Imahori & Kato, 1961) and New Zealand (Hotchkiss, in press). It suggests the possibility of a polyploid series. By contrast, numbers for the similar *N. gracilis* were reported as 17 by Lindenbein (1927) and 34 by Karling (1926).

The local variants of *N. pseudoflabellata* form about six more or less distinctive categories, all of which appear to blend into one another. These include ones which are (1) glomerate, larger, denser upper whorls (spec. ad); (2) diffuse but uniform branching throughout (spec. a, h, x, aa, ac); (3) inflorescence-producing upper whorls reduced and isolated along an elongated axis, also coupled with branchlets being only 2-furcate (spec. k, p, r, v, w)—var. *mathuatae*<sup>9</sup> (*N. muthnatae* T.F.A.); (4) elongate, intermediate between 1 and 2, but with fewer furcations (spec. z); (5) bushy with very uniform, regular branchlets, with mature oogonia at central tip of each branchlet (spec. l, m, q, af); and (6) very small, 2-4 cm high, slender and delicate,

<sup>9</sup> *N. pseudoflabellata* var. *mathuatae* (T.F.A.) R.D.W., *comb. nov.* (basonym: *N. muthnatae* T. F. Allen (1887:211)).

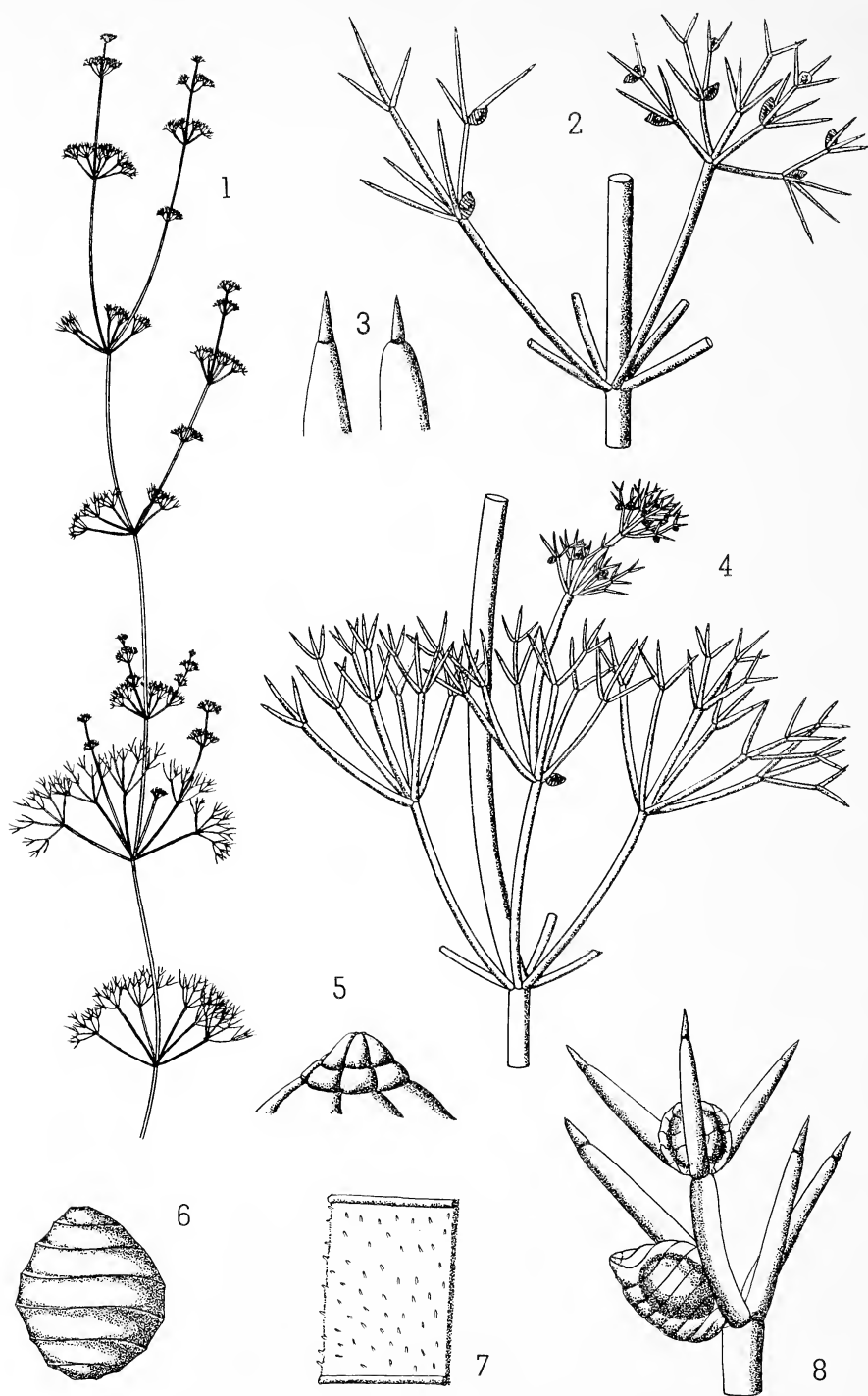


FIG. 5. Type of *Nitella mathuatae*, here designated as *N. pseudoflabellata* var. *mathuatae* (from Wood and Imahori, *Iconograph of the Characeae* (in press). Cramer. Weinheim (ICON 325)). 1, Habit,  $\times 1$ . 2, Axial node with (1-) 2-3-furcate fertile branchlets,  $\times 12$ . 3, End cells of dactyls,  $\times 90$ . 4, Lower axial node with 2-3-furcate branchlets and an accessory branch produced at the 1st node,  $\times 5$ . 5, Coronula,  $\times 390$ . 6, Oospore,  $\times 90$ . 7, Oospore membrane,  $\times 500$ . 8, Branchlet node with gametangia and dactyls,  $\times 40$ .

2-furcate (spec. e, t, u)—(*"N. Gibbsiae"* J. Gr., ined.). For convenience, these could be designated by such descriptive names as f. *glomerata*, *diffusa*, *mathuatae*, *elongata*, *fruticosa*, *minima*.

The original collections of *N. mathuatae* (as "*N. mutbnatae*") were distributed from the U. S. National Herbarium under the label of the United States Exploring Expedition and, aside from giving the location as "Muthnate Island" and the year as 1838–42, no data were added. Wilkes reported (1845:225, 234) that the ships anchored at "Muthuata Village" (Macuata) on June 19 and departed July 2, 1840. The entry concerning "Muthuata Island" (Macuata-i-wai) (*loc. cit.*, p. 230, 231) makes no mention of plant collecting. Thus, it is not clear when or by whom "*N. mutbnatae*" was gathered; but, as the specimens were well mounted and the ship was in Macuata for a limited time, it is here arbitrarily assumed that they were done by the botanists, Rich and Brackenridge, in June 1840. The exact location is not specified, but Macuata-i-wai is a small island less than a mile long, and in 1961 was said by the natives to have four creeks with standing-water holes. Concerning Macuata, it is curious that Derrick (1957) described it as deserted, rocky, and dense with *Casuarina* trees; that Wilkes (1845) described it as uninhabited and used for burials; whereas, in 1961, it had remnants of an extensive village, was reported as the stronghold of paramount chiefs, and had grassy upland with a coastal belt of coconut trees. Could there have been another Macuata just off Vanua Levu?

**HABITATS:** Rice fields, taro patch, drainage ditch, pool by bridge, pool below waterfall, pool behind beach, streams, and creeks.

**DISTRIBUTION:** In Fiji, collected on Viti Levu (Colo North, Lautoka, Nadroga, Naitasiri, Rewa, and Serua), Ovalau, and Vanua Levu (Macuata and Macuata-i-wai). *N. pseudoflabellata* is widespread in the eastern hemisphere and is known from Madagascar, India, Ceylon, Burma, China, Japan, Malaysia, New Caledonia, New Zealand, and Fiji.

**SPECIMENS:** OVALAU ISLAND: (a) *R. D. Wood and Bernard Vunibobo* 61–6–13–1. June

13, 1961. In ca. 3 inches of clear, flowing water, drainage ditch on village green, Nacobo Koro, ca. 6.4 miles along road S from Levuka (RDW 1567, Fig. 4) (CYT F 2,  $n = 18$ ; delicate, 3-furcate into 5–6 secondaries one of which is central, 4 tertiaries, 3 quaternaries); VANUA LEVU: Macuata: (b) *R. D. Wood and Vakuru Waibuta* 61–6–29–2A. June 29, 1961. In ca. 6 inches of water, mud bottom, ricefield W of Nakoroutari Road, ca. 2 miles S of Nakama Road, ca. 5 miles S of Labasa (oospores  $300 \times 210 \mu$ , striae 5, flanged, fossa  $63 \mu$  across, membrane granular-papillate, ca. 10 papillae across fossa; mixed with *C. corallina*);—(c) *ibid.* 61–6–29–3. *Ibid.* (antheridia ca.  $224 \mu$  in diam);—(d) *ibid.* 61–6–29–5. *Ibid.* (formal. only; mixed with *C. corallina*);—(e) *ibid.* 61–6–29–6A. *Ibid.* (formal. only; mixed with *C. corallina*) ("*N. gibbsiae*" J. Gr., CYT F 17,  $n = 18$ ; tiny, with dense terminal heads);—(f) *ibid.* 61–6–29–7. *Ibid.* (formal. only; mixed with *C. corallina*; gelatinous heads, ca.  $2 \times 1.5$  mm);—(g) *ibid.* 61–6–29–7A. *Ibid.* (crumbled to fragments);—(h) *ibid.* 61–6–29–8. *Ibid.* (nodes frequently swollen, branchlets stiff and straight, CYT F 18,  $n = 18$ );—(i) *ibid.* 61–6–30–10. June 30, 1961. Abundant in ca. 1 ft of clear water, silty-sandy-mud bottom, pool known as "Nalioniga" W of road ca. 1 mile past Seaqaqa Agric. farm (mixed with and labeled *C. corallina*);—(j) *ibid.* 61–6–30–11. *Ibid.* (formal. only; mixed with *C. corallina*);—(k) *ibid.* 61–6–30–12. *Ibid.*, but common in 10 inches of water (RDW 1544, Fig. 1) (exhibits inflorescence-like upper axial whorls);—(l) *ibid.* 61–6–30–12A. *Ibid.* (formal. only; no heads nor mucus, mature ♀ and ♂); Macuata-i-wai [Mathuata Island]: (m) *ibid.* 61–6–30–2. Common at margin in ca. 10 inches of clear water, sandy bottom, pool in creek [on hill side] at place known locally as "Vuniwesi" in shallow valley ca.  $\frac{1}{4}$  the way around S edge of island from koro [at NE point] (soft and delicate branchlets, fossae ca.  $42 \mu$  across);—(n) *ibid.* 61–6–30–3. *Ibid.* (formal. only; mucus heads, variable branchlets (some simple), oogonium  $440 \times 354 \mu$ , convolutions 9, coronula  $20 \times 50 \mu$  wide, upper cells slightly longer than lower, oospore brown, fossa ca.  $46 \mu$  across, membrane

loosely papillate, ca. 10 papillae across fossa and 2–3 diameters apart on roughened background); —(o) *ibid.* 61–6–30–4. *Ibid.* (formal. only; mixed with and labeled *C. fibrosa*) (typical f. *mathuatae*) TOPOTYPE; —(p) *ibid.* 61–6–30–5. Abundant, in ca. 3 inches of clear water, sandy mud bottom, at outflow from pool [location as above] (RDW 1541, Fig. 4) (CYT F 20x, n = 18; formal. specimen with heads ca. 5 mm in diam, antheridia 160–280  $\mu$  in diam, dactyls unequal, secondary and tertiary rays occasionally simple, typical f. *mathuatae*) TOPOTYPE; —(q) *ibid.* 61–6–30–6. *Ibid.*, but in ca. 10 inches of clear water; —(r) [*? W. Rich and J. D. Brackenridge*] s.n. June, 1840. In small pool in creek. Muthuate Island, Feejee. (as U. S. South Pacific Expl. Expedition under Command of Capt. Wilkes. 1838–1842). (US, HOLOTYPE; NY, ISOTYPE, Fig. 5). Note: the script is easily misinterpreted to read “Muthnate,” as apparently was done by T. F. Allen (1887: 211); VITI LEVU: Colo North: (s) *L. S. Gibbs* 762. July 10, 1909 (Sept. 1907). In stream, Mt. Waikubakuba [–] Tabua Rd., 500 ft alt, Nadarivatu (K, as *Nitella gracilis*, det. ?; poor wadded specimen); LAUTOKA: (t) *W. Greenwood* 102. Aug. 29, 1920. In water in taro plantation, Mt. Lautoka (K, as *Nitella* sp., annotated “*N. Gibbsiae*, J. Groves ms”); —(u) *ibid.* 103. *Ibid.* (K, *ibid.*); NADROGA: (v) *R. D. Wood* 61–6–11–1. June 11, 1961. In ca. 12 inches of clear water, mud bottom, drained rice paddy, ca. 14 miles N of Cuvu on Queen’s Road; Naitasiri: (w) *R. D. Wood and S. Pillay* 61–6–26–1. June 26, 1961. In ca. 6 inches of rather turbid water, mud bottom, small pool ca. 200 ft SE of S end of bridge at Sawani, ca. 18 miles N of Suva; —(x) *S. Pillay and A. Vualili*, Suva 12501. July 12, 1961. Scarce, muddy water, in pool at base of waterfall, Sawani; Rewa: (y) *B. Vunibobo*, Suva 12502. June 25, 1961. Standing water, ricefield at Dreketi midway between Vunisinu and Nadona village (glomerate variant); —(z) *R. D. Wood* 61–7–5–1. July 5, 1961. Sparse in ca. 6 inches of turbid water, mud bottom, field pool ca. 50 ft S of King’s Road, between road and Rewa River, ca. 2 miles NW of Nausori; Serua: (aa) *I. Bola*, Suva 12503. July 17, 1961. Wairoro Creek, Nabukavesi; —(ab) *ibid.*, Suva 12504. *Ibid.*—

(ac) *ibid.*, Suva 12505. July 18, 1961. Scarce, Nabukavesi Creek; —(ad) *ibid.*, Suva 12506. July 19, 1961. *Ibid.*; —(ae) *R. D. Wood* 61–6–25–5A. June 25, 1961. In ca. 8 inches of clear, fresh water, fairly firm mud bottom, pool ca. 50 ft behind beach, ca. 500 yards S of jetty at end of Naitonitoni Road, ca. 31 miles W of Suva; —(af) *ibid.* 61–6–25–6. *Ibid.* (RDW 1554, Fig. 4) (CYT F 11, n = 18).

#### CONCLUSIONS

1. Intensive collecting of Characeae on four islands of the Fiji group was done in June–July, 1961, and two genera and five distinct species, including *Chara corallina*, *C. fibrosa*, *Nitella acuminata*, *N. furcata*, and *N. pseudoflabellata*, were found.

2. The two earlier reports were of *Chara australis* and *Nitella mathuatae* (as *muthnatae*); but, through revision, these are included as synonyms of *C. corallina* and *N. pseudoflabellata*, respectively.

3. The chromosome numbers were found to be: *C. corallina* (dioecious state) 14, *C. fibrosa* 28, *N. acuminata* 18, and *N. pseudoflabellata* 18. No counts were made of *N. furcata* on Fiji, but the same species in Samoa had 18.

4. The chromosome numbers are, with the exception of *N. pseudoflabellata*, consistent with findings for the species in other countries, and add confirmation to the writer’s new classification system.

5. Certain of the habitats in which Characeae occur in Fiji are also found in the Society Islands; and thus the absence of these plants from Tahiti is probably not due entirely to lack of suitable environments.

6. *Nitella* is somewhat more common than *Chara* in number of habitats occupied (56.2% of the habitats with Characeae had *Nitella* and 43.8% had *Chara*).

7. Characeae occurred in 19% of the habitats examined, predominating in rice fields and in ponds in fields and open woods. They were rare in taro patches, streams, and rivers.

8. *Nitella mathuatae* T.F.A. is transferred to *N. pseudoflabellata* var. *mathuatae* (T.F.A.) R.D.W., comb. nov.

## COLLECTORS AND COLLECTORS' NUMBERS

Species number and specimen letter as they appear in the text are cited in parentheses.

BOLA: 12503 (5aa), 12504 (5ab), 12505 (5ac), 12506 (5ad)—GIBBS: 762 (5s)—GREENWOOD: 102 (5t), 103 (5u), 104 (2g)—NAUMANN: s.n. (1a)—PARHAM: 742 (1u)—PILLAY and VUALILI: 12498 (1s), 12499 (1t, 4b), 12500 (4c), 12501 (5x)—PILLAY and WOOD: (see Wood and Pillay)—RICH and BRACKENRIDGE: s.n. (5r)—SMITH: 6698 (1d)—U. S. SOUTH PACIFIC EXPLORING EXPEDITION (see Rich and Brackenridge)—VUALILI (see Pillay and Vualili)—VUNIBOBO: 12502 (5y) (also see Wood and Vunibobo)—WAIBUTA (see Wood and Waibuta)—WEBER: 573 (1b)—WOOD: 61611 (1c), 616111 (5v), 616112 (2i), 616113 (2j), 616114 (2k), 616251 (3e), 616252 (3f), 616253 (3g), 616255 (3h), 616255A (5ae), 616256 (5af), 616259 (3j), 616266 (5af), 616281 (2l), 616282 (2m), 616751 (5z), 61681 (3c), 61682 (3d), 61691 (2h), 61711 (1c), 61751 (5z)—WOOD and FAMILY: 61791 (1r)—WOOD and PILLAY: 616261 (5w), 616262 (3a), 616263 (3b), 616264 (4a)—WOOD and VUNIBOBO: 616131 (5a)—WOOD and WAIBUTA: 616291 (1e, 2a), 616292 (1e), 616292A (5b), 616293 (5c), 616294 (1f), 616295 (1g, 5d), 616296 (1h), 616296A (5e), 616297 (1i, 5f), 616297A (5g), 616298 (5h), 616299 (1j), 6162910 (1k), 6162911 (1l), 616301 (2b, 1q), 616302 (2c, 5m), 616303 (2d, 5n), 616304 (2e, 5o), 616305 (5p), 616306 (5q), 616306A (2f), 6163010 (5i, 1m), 6163011 (1n, 5j), 6163012 (5k), 6163012A (1o, 5d), 6163012C (1p).

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# Chromosome Numbers in Characeae from the South Pacific<sup>1</sup>

ARLAND HOTCHKISS<sup>2</sup>

**ABSTRACT:** This study of a total of 18 collections represents the first sampling of chromosome numbers in the charophytes from New Caledonia, Fiji, and Samoa. Chromosome counts were obtained for the first time for material of *Lamprothamnium* (*Chara*) *succinctum*, and the count supports the transfer to the genus *Lamprothamnium*. Chromosome counts consistent with earlier reports are those of 14 for the dioecious taxa included in *Chara corallina* (*Chara australis*, *Protochara australis*, *Chara fulgens*) by Wood, and 18 for *Nitella acuminata*. Not in accord with some earlier reports are the counts of 18 for *Nitella hyalina*, 18 for *Nitella pseudoflabelata* (including *N. mathuata*), 18 for *Nitella furcata*, and 28 for *Chara fibrosa*.

The presence of somatic pairing of chromosomes is noted in *Chara fibrosa*, and the extent and importance of polyploidy in the charophytes is recalled.

THE EXTENSIVE COLLECTIONS of charophytes made by Dr. R. D. Wood during the course of an expedition ranging from Australia to New Zealand and islands of the South Pacific in 1960–61 will form an important basis for studies on the Characeae of these regions. As already reported (Wood, 1962*b*) the collections include plant specimens gathered and preserved especially for cytological examination. These the writer was privileged to receive, together with the accompanying field notes and identifications which follow the revision of the group by Wood (1962*a*). This paper, the first in a series to record the chromosome numbers and related cytological findings in the Wood collections, is concerned with the plants from New Caledonia, Fiji, and Samoa, and is concurrent with detailed taxonomic treatments of these plants by Wood (1963, 1965). Although the present paper is complementary in nature no attempt has been made to support all the taxonomic conclusions in Wood's revision of the Characeae.

## PLANT MATERIALS AND METHODS

For the cytological studies, fertile plants with growing tips bearing young stages of gametangial development were selected and fixed in the field. In dioecious species only the male plants are required for the young antheridia used

in making chromosome counts. Fixation with freshly prepared acetic-alcohol was done in the usual manner. The specimens were then transferred to 70% ethanol and shipped in sealed vials by airmail to Louisville, where they were stored under refrigeration. Chromosome counts were made from mitoses found in squashed preparations of filaments dissected from the antheridia and stained with aceto-orcein. Usually a series of preparations were needed before a count could be determined with certainty. Drawings were made with the aid of a camera lucida.

Four vials of specimens were received from New Caledonia, 12 from Fiji, and 1 from Samoa, each of which yielded chromosome counts. All these specimens and the permanent slides of chromosome preparations made from them are deposited in the Herbarium of the University of Louisville; other parts of these collections are deposited elsewhere (Wood, 1962*b*).

The collection data listed below include the notes supplied by Dr. Wood as to dates, localities, ecology, and collecting numbers. The cytology collection numbers (CYT) were included with the notes and on the cork stoppers of the

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vials sent to Louisville. All these data are included here in an effort to maintain a maximum correlation between our sometimes fragmentary materials and the main collections of complete plants.

#### COLLECTIONS FROM NEW CALEDONIA

1. *Chara corallina* Klein ex Willd. em. R. D. W.<sup>3</sup>

R. D. Wood 61-6-20-8. June 20, 1961. In c. 4" of fairly clear water, mud bottom, field pool SE of "Dumbea Barrage Road" c. 2.5 km N of W Coast road New Caledonia. (CYT NC-5.)

2. *Lamprothamnium succinctum* (A. Br. in Asch.) R. D. W.

R. D. Wood 61-6-20-1. June 20, 1961. In c. 8" of brackish water, fairly turbid, soft mud bottom, SE side about  $\frac{2}{3}$  way to NE end on Marsh "Hippodrome," Noumea, New Caledonia. (CYT NC-1.)

3. *Lamprothamnium succinctum* (A. Br. in Asch.) R. D. W.

R. D. Wood 61-6-20-4. June 20, 1961. In c. 8" of brackish, fairly turbid water, soft mud bottom, SE side of marsh c.  $\frac{2}{3}$  way to NE end, "Hippodrome," Noumea, New Caledonia. (CYT NC-2.)

4. *Nitella hyalina* (DC) Ag.

R. D. Wood 61-6-20-6. June 20, 1961. In c. 4" of fairly clear water, mud bottom, field pool SE of "Dumbea Barrage Road," c. 2.5 km N of W coast road, New Caledonia. (CYT NC-3.)

#### FII

1. *Chara corallina* Klein ex Willd. em. R. D. W.

R. D. Wood & Vakuru Waibuta 61-6-29-6. June 29, 1961. In c. 6" of clear water, mud bottom, pool in dry ricefield, W of Nakoroutari Rd., c. 2 mi. S of Nakama Rd., probably c. 5 mi. S of Labasa, Vanua Levu, Fiji. (CYT Fiji-17.) (In collection primarily of *C. fibrosa*.)

2. *Chara corallina* Klein ex Willd. em. R. D. W.

R. D. Wood 61-7-1-1. July 1, 1961. Abundant in 1-2 ft. of fairly clear water, mud bottom, large pool c. 100 ft. SE of Loa Rd. c. 26 mi. E of Savusavu airport, Cakadrove Peninsula, Vanua Levu, Fiji (at culvert L284). (CYT Fiji-20.)

<sup>3</sup> em. Wood, 1962, to include both dioecious and monoecious forms, thus uniting *C. australis* and *C. corallina* in one taxon.

3. *Chara corallina* Klein ex Willd. em. R. D. W. R. D. Wood & Vakuru Waibuta 61-6-29-1. June 29, 1961. In c. 3" of clear water, mud bottom, pool in drained ricefield W of Nakoroutari Rd., c. 150 ft. W of culvert marker K33, probably c. 5 mi. S of Labasa, Vanua Levu, Fiji. (CYT Fiji-16.)

4. *Chara fibrosa* Ag. ex Bruz.

R. D. Wood 61-6-9-1. June 9, 1961. In c. 6" of fairly clear water, mud bottom, pond in marsh, N side of Queen's Road, c. 1 mi. W of Sigatoka Hotel, Viti Levu, Fiji. (CYT Fiji-1.)

5. *Chara fibrosa* Ag. ex Bruz.

R. D. Wood 61-6-28-1. June 28, 1961. Large mass in c. 6" of clear, fresh water, black muck bottom, small ditch pool on W side of Natovi-Korovou Rd., c. 13 mi. N of Korovou, Viti Levu, Fiji. (CYT Fiji-15.)

6. *Nitella acuminata* A. Br. ex Wallm.

R. D. Wood 61-6-25-1. June 25, 1961. In 3-4" of clear water, mud bottom, wet field N of road, c.  $\frac{1}{4}$  mi. N of Navua Hotel, Navua, Fiji (c. 28 mi. W of Suva). (CYT Fiji-10.)

7. *Nitella acuminata* A. Br. ex Wallm.

R. D. Wood & S. Pillay 61-6-26-3. June 26, 1961. In c. 12" of fairly turbid water, mud bottom, amid water lilies, in the western of the two large lily ponds on the plain below Adi Cakabou School, Sawani (c. 18 mi. N of Suva), Fiji. (CYT Fiji-14.)

8. *Nitella pseudoflabellata* A. Br. em., glomerate form.

R. D. Wood & Bernard Vunibobo 61-6-13-1. June 13, 1961. In c. 3" of clear flowing water, mud bottom, drainage ditch in village green, Nacobo Koro, c. 6.4 mi. S of Levuka, Ovalau, Fiji. (CYT Fiji-2.)

9. *Nitella pseudoflabellata* A. Br. em., fruticose form.

R. D. Wood 61-6-25-6. June 25, 1961. In c. 8" of clear, fresh water, fairly firm mud bottom, pool c. 50 ft. behind beach c. 500 yd. S of jetty, Naitonitoni, Viti Levu, Fiji (c. 31 mi. W of Suva). (CYT Fiji-11.)

10. *Nitella pseudoflabellata* A. Br. em., tiny form.

R. D. Wood & Vakuru Waibuta 61-6-29-6. June 29, 1961. In c. 6" of clear water, mud bottom, pool in dry ricefield, W. of Nakoroutari

Rd., c. 2 mi. S of Nakama Rd., probably c. 5 mi. S of Labasa, Vanua Levu, Fiji. (CYT Fiji-17.)

11. *Nitella pseudoflabellata* A. Br. em., diffuse form.

R. D. Wood & Vakuru Waibuta 61-6-29-8. June 29, 1961. In c. 6" of clear water, muck bottom, pool in dry ricefield, W of Nakoroutari Rd., c. 2 mi. S of Nakama Rd., probably c. 5 mi. S of Labasa, Vanua Levu, Fiji. (CYT Fiji-18.)

12. *Nitella pseudoflabellata* A. Br. em., var. *mathuata* (T.F.A.) R.D.W.

R. D. Wood & Vakuru Waibuta 61-6-30-5. June 30, 1961. Abundant in c. 3" of clear water, sandy mud, overflow stream from pool in creek at place known as "Vuniwesi" in valley c. 1/4 way around S side of island from NE end, Mathuata-i-wai Island, Vanua Levu, Fiji. (CYT Fiji-20X.)

13. *Nitella pseudoflabellata* (duplicate of CYT Fiji-20X.)

SAMOA

1. *Nitella furcata* (Roxb. ex Bruz.) Ag. var. *sieberi* (A. Br.) R. D. W.

R. D. Wood, Ed. Tia'i & Esekia Sei'a 61-8-1-1. August 1, 1961. (CYT Samoa-1.)

CHROMOSOME NUMBERS

The chromosome counts together with the collection numbers from this study are listed in Table 1 in the same sequence followed in listing the collection data. The numbers are gametic numbers taken from mitoses in the antheridial filaments prior to formation of the sperm. Illustrations of the chromosomes of each species are shown in Figures 1 and 2.

DISCUSSION AND CONCLUSIONS

As is to be expected some of the chromosome numbers recorded here represent unreported species, while others either confirm previous counts or are at variance with those of previously published numbers. There is a total of five new counts.

In the revision of Wood (1962a) many well-known species have been reduced to lower taxa. Notes connecting the revision names with the older usage are provided in the following discussion of individual species and collections.

TABLE 1  
CHROMOSOME NUMBERS IN CHAROPHYTES FROM THE SOUTH PACIFIC  
(By A. and D. Hotchkiss)

SPECIES ( <i>sensu</i> Wood, 1962a)	<i>n</i>	COLLECTION NUMBERS	FIGURE
NEW CALEDONIA			
1. <i>Chara corallina</i>	14	61-6-20-8 (CYT NC-5)	1a
2. <i>Lamprothamnium succinctum</i>	42	61-6-20-1 (CYT NC-1)	1e
3. <i>L. succinctum</i>	42	61-6-20-4 (CYT NC-2)	1f
4. <i>Nitella hyalina</i>	18	61-6-20-6 (CYT NC-3)	1j
FIJI			
1. <i>Chara corallina</i>	14	61-6-29-6 (CYT Fiji-17) *	1b
2. <i>C. corallina</i>	14	61-7-1-1 (CYT Fiji-20)	1c
3. <i>C. corallina</i>	14	61-6-29-1 (CYT Fiji-16)	1d
4. <i>C. fibrosa</i>	28	61-6-9-1 (CYT Fiji-1)	1g
5. <i>C. fibrosa</i>	28	61-6-28-1 (CYT Fiji-15)	1b, i
6. <i>Nitella acuminata</i>	18	61-6-25-1 (CYT Fiji-10)	2a, b
7. <i>N. acuminata</i>	18	61-6-26-3 (CYT Fiji-14)	2c
8. <i>N. pseudoflabellata</i>	18	61-6-13-1 (CYT Fiji-2)	2d, e
9. <i>N. pseudoflabellata</i>	18	61-6-25-6 (CYT Fiji-11)	2f, g
10. <i>N. pseudoflabellata</i>	18	61-6-29-6 (CYT Fiji-17) *	2b
11. <i>N. pseudoflabellata</i>	18	61-6-29-8 (CYT Fiji-18)	2i
12. <i>N. pseudoflabellata</i>	18	61-6-30-5 (CYT Fiji-20X)	2j
13. <i>N. pseudoflabellata</i>	18	61-6-30-5 (CYT Fiji-20X duplicate)	
SAMOA			
1. <i>Nitella furcata</i>	18	61-8-1-1 (CYT Samoa-1)	1k

\* A mixed collection.



FIG. 1. Metaphase chromosomes in antheridial filaments of charophytes from the South Pacific. a-d, *Chara corallina* (sensu Wood, 1962a); e-f, *Lamprothamnium succinctum*; g-i, *Chara fibrosa*; j, *Nitella hyalina*; k, *Nitella furcata*. (Camera lucida drawings, all X 900.)

#### New Caledonia

##### 1. *Chara corallina* (CYT NC-5). Figure 1.

Plants ecorticate, dioecious, with basal gametangia, have the combination of characters of *Chara australis*; the inflated axes and generally lacking or reduced lateral appendages more narrowly suggest *Protochara australis*. In correspondence Wood notes,

"CYT 5 . . . I find to be *Chara corallina* (dioecious strain)—the *C. australis* of earlier workers, in part). You have '*Protochara australis*,' but the specimens I have from New Caledonia are not nearly so inflated as the ones I've seen from Australia."

The chromosome number 14 is to be expected

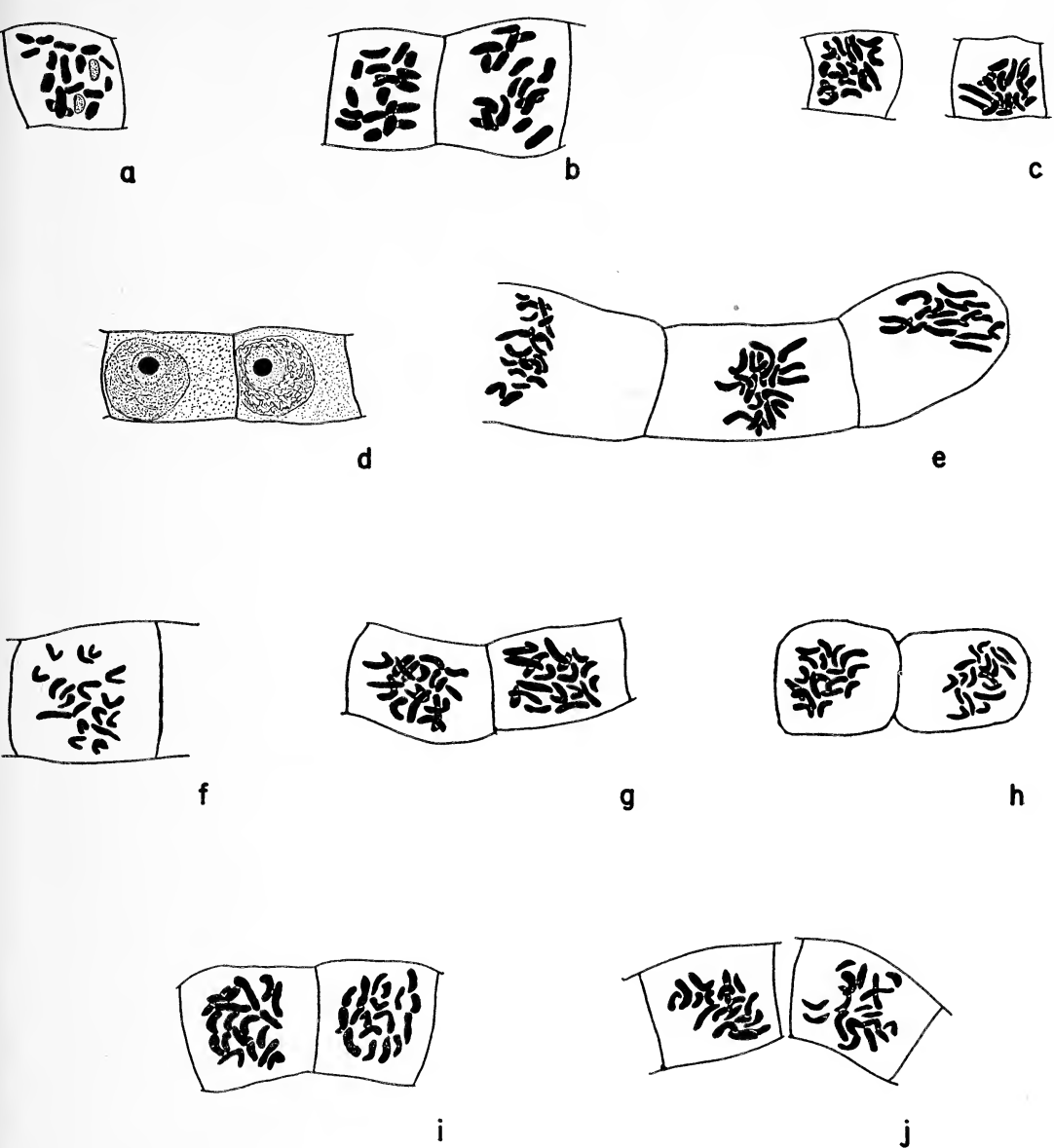


FIG. 2. Chromosomes in antheridial filaments of charophytes from the South Pacific. *a-c*, *Nitella acuminata* metaphase; *d-j*, *Nitella pseudoflabellata*; *d*, interphase, *e-j*, metaphase. (Camera lucida drawings, all X 900.)

in all members of the Haplostephanae-ecorticatae; the count recorded here confirms the previous counts of 14 in the dioecious *Chara* (*Protochara*) *australis* from Australia (MacDonald and Hotchkiss, 1955).

2-3. *Lamprothamnium succinctum* (CYT NC-1 and 2). Figure 1e, f.

The present count of 42 chromosomes is a

first report for this species. The high number of 42 agrees generally with another count for this genus, that of Lindenbein (1927) which was ca. 50 for *Lamprothamnium papulosum* (Wallr.) J. Groves. The number and general configuration of the chromosomes lend support to Wood's (1962a: 14) transfer of *C. succinctum* to the genus *Lamprothamnium*.

4. *Nitella hyalina* (CYT NC-3). Figure 1j.

The report of 18 chromosomes here confirms our unpublished counts of 18 chromosomes in this species from North Carolina and Mexico. A count of 16 was proposed by Gillet (1959) and the numbers 12, 14, 18 have all been reported by Sato (1959), but we have seen no tendency towards such variations in *Nitella hyalina*.

## Fiji

1-2. *Chara corallina* (CYT Fiji-17 and 20). Figure 1b, c.

Both specimens are ecorticate, dioecious, with basal gametangia and lateral appendages and fall in the earlier category of *Chara australis*. The chromosome count of 14 confirms the counts for this species (MacDonald and Hotchkiss, 1955).

3. *Chara corallina* (CYT Fiji-16). Figure 1d.

A lack of gametangia at the base of the branchlets in our material suggested the characters of *Chara fulgens* Fil. in Asch.<sup>4</sup> except for the geminate and not solitary gametangia. This combination of characters fills one of the blank spaces in the table of *Homologous Variations in the Haplostephaniae-ecorticatae* of *Chara* of Zaneveld (1940).

4-5. *Chara fibrosa* (CYT Fiji-1 and 15). Figure 1g, h, i.

Following the treatment of Zaneveld (1940), Wood notes that this includes *Chara gymnopyris* A. Br. of earlier authors. A count of 28 chromosomes is a first report for this species and is to be compared with our unpublished counts of 42 for this species from North Carolina.

6-7. *Nitella acuminata* (CYT Fiji-10 and 14). Figure 2a, b, c.

Wood (1965) recognizes a dendroid and a lax ecad; No. 14 is the dendroid and No. 10 is the lax variant. They seem to overlap typical var. *acuminata*. The chromosomes of *N. acuminata* are somewhat similar in form to those of *N. pseudoflabellata*, but these two species can be separated on the basis of chromosome form.

<sup>4</sup> Wood (correspondence in 1963) includes *C. fulgens* in *C. corallina*; in Fiji he reports the occurrence or absence of basal oogonia to be sporadic in otherwise identical specimens, which further confirms his opinion.

Counts of 18 have been reported previously for *N. acuminata* var. *subglomerata* by Hotchkiss (1958), Imahori and Kato (1961).

8-13. *Nitella pseudoflabellata* (CYT Fiji-2, 11, 17, 18, 20X). Figure 2d-j.

Wood (1965) detects six ecads or forms and provides noncommittal names. They include (1) glomerate (*glomerata*), (2) diffuse (*diffusa*), (3) mathuate (var. *mathuata*, olim *N. muthnatae*), (4) elongate (*elongata*), (5) bushy (*fruticosa*), and (6) tiny (*minima*). CYT Fiji-2 is the glomerate, CYT Fiji-11 is the bushy, CYT Fiji-17 is the tiny, CYT Fiji-18 is the diffuse, and CYT Fiji-20X is the mathuate variant.

The only record of a chromosome count in *N. pseudoflabellata* is a 24 reported from Japan (Imahori and Kato, 1961). Although an expected number in *Nitella*, reports of 24 chromosomes have been surprisingly few.

## Samoa

1. *Nitella furcata* (CYT Samoa-1). Figure 1k.

A count of 18 chromosomes in this species from Samoa is at variance with a report of 24 (and 48) chromosomes by Imahori and Kato (1961) from Japan.

It is noted again that the number of 14 chromosomes is the smallest yet found for any species of *Chara* and that the dioecious species reported here have this number. The correlation between the dioecious condition of sex distribution and low chromosome number (Hotchkiss, 1958) continues to hold, but its significance in relationships in the Haplostephaniae-ecorticatae (Section Charopsis of Wood's revision) is obscured by finding the same number in all species of this group, whether monoecious or dioecious, studied thus far.

In the chromosome complements of charophytes, pairs of chromosomes of similar length and form are often seen. In these cases, and as noted in the present study in *Chara fibrosa* (Fig. 1b, i), there seems to be more than a chance positioning of homologous chromosomes, suggesting a high degree of somatic pairing. The common appearance of chromosomes in multiples of 6 and 9 (in series of *Nitella* species), and in multiples of 14 (in species of *Chara*), indicates the extent and importance of polyploidy in this group of "lower" plants. Additional cyto-

logical features of note include the usual interphase nuclei with nucleoli shown in Figure 2*d* (*Nitella pseudoflabellata*), and a pair of "gray," lightly stained chromosomes apparently lagging in development in *Nitella acuminata* (Fig. 2*a*).

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# A Study of Stomatal Structure in Pandanaceae

P. B. TOMLINSON<sup>1</sup>

**ABSTRACT:** Many species of Pandanaceae have unspecialized stomata. In species of *Pandanus* there is a range of stomatal structure involving increasing elaboration of papillae arising from subsidiary and neighbouring cells so that guard cells, which are otherwise constant in structure throughout the family, are increasingly provided with a canopy of papillae which, together with sinking of the stomatal apparatus, produces an outer stomatal chamber. In the most specialized stomata this chamber is itself virtually occluded by lobed papillae.

*Freycinetia* may show significant differences from *Pandanus*. This linear trend of specialization can often be partly or wholly demonstrated on a single individual because stomata are always unspecialized on the first scalelike leaves of each renewal shoot, thereafter being increasingly specialized on subsequent leaves until the maximum *potential* elaboration characteristic of the species is realised on foliage leaves. This is briefly discussed in relation to taxonomy, physiology, and ecology.

THIS ARTICLE is the partial result of a recent study of the systematic anatomy of the Pandanaceae in which limited material of all three of its genera, *Freycinetia*, *Pandanus*, and *Sararanga*, has been examined. Insufficient material has been studied to permit worthwhile comment about the diagnostic value within the family of microscopic structures, except that anatomy is relatively uniform throughout the Pandanaceae and emphasizes its naturalness. In the survey a considerable range in stomatal structure was found, especially in *Pandanus*, a range not fully described by previous observers like Köfler (1918), Solla (1884), or Solereder and Meyer (1933). Observations were extended to indicate the range of stomatal structure throughout a single plant, whereupon it was discovered that, in certain instances, the full range of stomatal variation within the genus could be demonstrated within a single individual. This can be explained when the growth habit of *Pandanus* is understood.

It was felt that a general summary of stomatal structure in Pandanaceae would be a significant contribution to the literature on monocotyledonous anatomy. The present account deals

largely with *Pandanus*, notes on *Freycinetia* and *Sararanga* being included when they show outstanding features. Material of some 50 species has been examined during the course of this study, which—in view of the richness of *Pandanus*, estimated at 500–600 species, and of *Freycinetia*, at 180–200 species (St. John, 1960)—indicates how provisional this study is. It is not, therefore, intended as an exhaustive survey of the subject, but gives a clear indication of the known range of stomatal structure in Pandanaceae and points the way to more intensive study.

## MATERIAL AND METHODS

The survey is largely based on herbarium material of *Pandanus* supplied from specimens in the Bernice P. Bishop Museum, Honolulu, Hawaii, by Dr. B. C. Stone, the material being selected to represent a wide range of subgenera. It was supplemented by material collected by myself and others in the wild, and by material in cultivation at the Fairchild Tropical Garden and the U. S. Department of Agriculture Experiment Station, Old Cutler Road, Miami, Florida. Slides and specimens in the collections of the Jodrell Laboratory, Royal Botanic Gardens, Kew,

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England, have also been examined. The cultivated material was in many instances unnamed and was used largely to confirm observations on named species and to provide large samples for studies in stomatal variability. Observation on unnamed species, with few exceptions, has not been tabulated in this account. A full list of named material and sources is given in the appendix.

Only simple technical methods have been used. Dried material was restored to a consistency suitable for anatomical study by boiling for several minutes in water to which a little Clorox was added. This revived material was stored in formalin-acetic-alcohol and proved quite satisfactory for anatomical study. Some distortion which could not be eliminated by the reviving technique did not obscure anatomical details. This point is emphasized, because it means that stomatal studies in Pandanaceae can proceed satisfactorily using herbarium material. Fresh material has been examined either unfixed or fixed in formalin-acetic-alcohol.

Preparations showing the surface layers in surface view were made by the simple scraping technique employed at the Jodrell Laboratory and described in detail by Metcalfe (1960:lx). Such preparations were either made permanent in Canada Balsam, after staining in safranin and Delafield's haematoxylin, or were examined as temporary mounts in chlor-zinc-iodide. All material to be sectioned was desilicified by soaking overnight in 50% hydrofluoric acid, followed by prolonged washing in running water. Freehand sections of the demineralized but unembedded material, in 70% alcohol, were cut at 10–20  $\mu$  in transverse and longitudinal sections on a Reichert sliding microtome. Most observations were made on sections in temporary glycerine mounts, either unstained or after treatment with a variety of temporary stains, such as phloroglucin and concentrated hydrochloric acid, Sudan IV, chlor-zinc-iodide, iodine-potassium iodide, and 70% sulfuric acid. A few permanent preparations of the freehand sections were made by a method described elsewhere (Tomlinson, 1961: 5).

Illustrations (Figs. 8–51) are from camera lucida drawings. These are somewhat stylized because of some persistent distortion in dried

material and because it was often possible to cut only thick sections. This is quite an advantage since they allowed a complete three-dimensional picture of stomata to be built up from optical sections in three planes at right angles.

GENERAL MORPHOLOGY OF PANDANACEAE

This has been described by Schumann (1897), Warburg (1900), and Schoute (1903, 1906) and summarized briefly by Tomlinson (1964). Some knowledge of growth habit and branching in Pandanaceae is essential for an understanding of variation in stomatal structure throughout a single individual. Early branching begins independently of flowering, but later branching is regular, sympodial, and largely dependent upon flowering. Lateral branches then arise below and replace a parent axis, growth of which is ended by its conversion into a terminal inflorescence. Eviction of terminal buds by one or more laterals is a method of branching typical of plants without secondary tissue (Schoute, 1906; Tomlinson, 1964). In Pandanaceae each lateral renewal branch in these sympodia bears a similar sequence of leaf forms (Fig. 1). The first leaf on a branch is always a short, bicarinate prophyll in the adaxial (adossierte) position. This is succeeded by a number of scale leaves, each successively longer than its predecessor, forming a gradual transition to the normal foliage leaves. Length of foliage leaves is fairly constant, although distal foliage leaves, close to the inflorescence, are short. Renewal buds, one or more of which grow out to form the next segments of the sympodium, are prominent in the axils of these distal leaves. Change of the vegetative into a reproductive axis is marked by elongation and narrowing of internodes. Inflorescence leaves, which are short foliage leaves with a narrow insertion on the lowest nodes of the inflorescence, may be distinguished (Schumann, 1897). Beyond them is a rapid transition to short, colorless bracts. The over-all leaf sequence illustrated diagrammatically in Figure 1 for one sympodial segment of a small *Pandanus* is characteristic for all Pandanaceae, although the number of leaves on each segment varies considerably, even within a single individual.

Foliage leaves are lanceolate. In *Pandanus* and

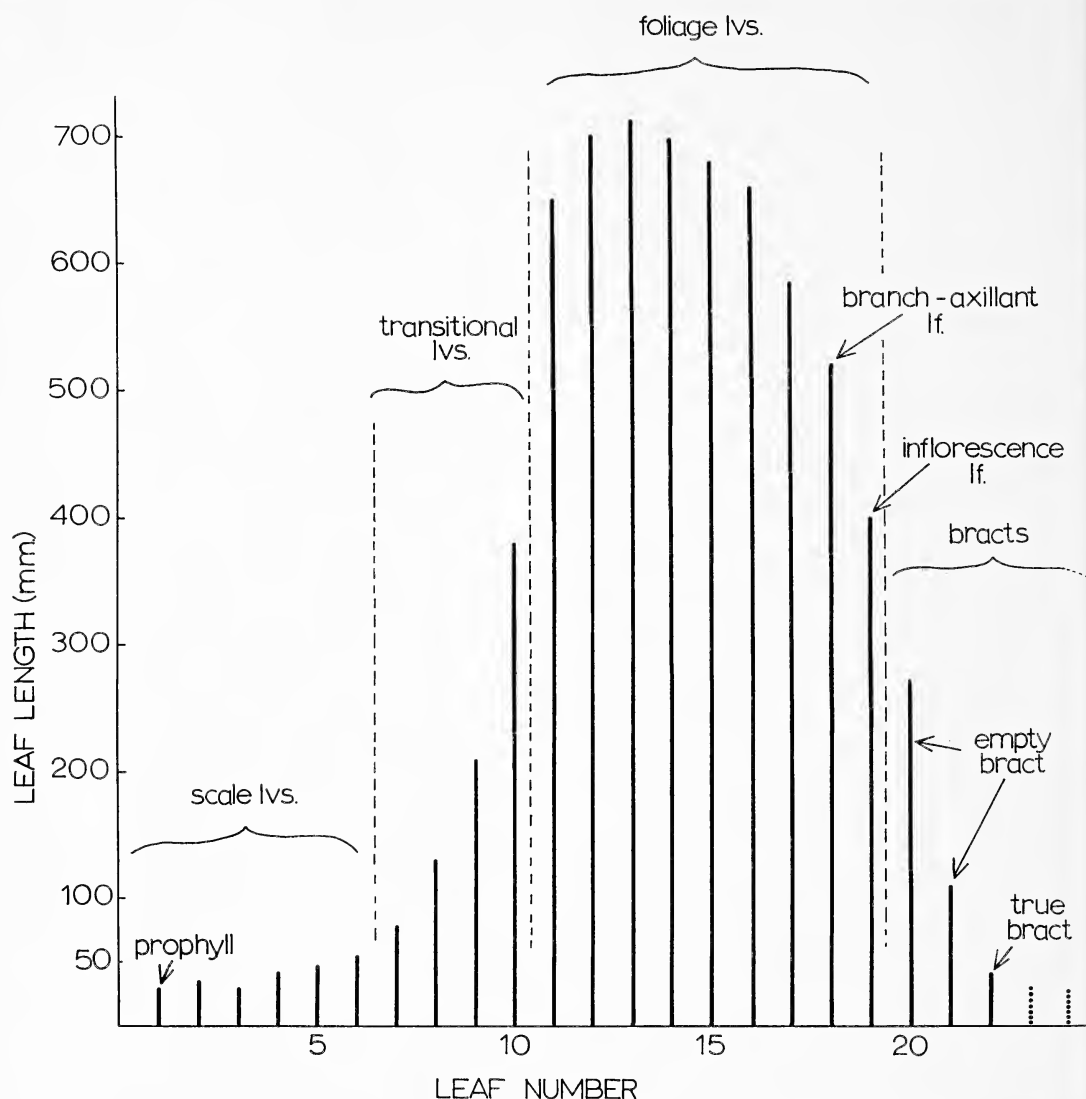


FIG. 1. Diagrammatic representation of change in leaf length along a single shoot in a diminutive species of *Pandanus* (P. I. 135008 U.S.D.A. Experiment Station, Miami, Florida).

*Sararanga* they more or less completely enclose the axis at their insertion without forming a closed tube; there is no distinction between blade and sheath. In *Freycinetia* there is a slight differentiation between a short basal sheathing region and a blade, the mouth of the open sheath being slightly auriculate.

#### GENERAL ANATOMY OF THE LEAF

Leaf anatomy is very uniform throughout the Pandanaceae so that all leaves are basically constructed alike, differences between different spe-

cies being largely quantitative.

The leaf is dorsiventral. Hairs are absent, although leaf margins and midrib usually bear prominent spines. Stomata are largely confined to the abaxial surface. The leaf is delimited by well-developed surface layers, each consisting of a shallow, strongly cutinized but never markedly thick-walled epidermis and well-developed, colourless, and often slightly thick-walled hypodermal layers, usually three or four cells deep. Adaxial hypodermal layers are usually somewhat thicker than abaxial. Epidermal cells are usually

rectangular, slightly longitudinally extended, and arranged in longitudinal files. In the abaxial, but not adaxial, epidermis distinct nonstomate costal regions below the veins are differentiated from intercostal regions, between the veins, to which stomata are restricted. There is no coincidence between epidermal and hypodermal files. Hypodermal cells contrast with epidermal in that their outermost two layers consist of flattened cells extended transversely and not longitudinally to the long axis of the leaf. Since epidermal cells are thus much narrower than hypodermal cells in the transverse direction, three or four files of epidermal cells occupy the space of one file of outer hypodermal cells (Fig. 2). Anticlinal walls in outer hypodermal layers do not coincide since their cells are clearly derived from different initial layers. The outermost hypodermal layers often become sclerotic; the inner cells in contrast are larger, more cubical in shape, and usually remain thin-walled. Hypodermal layers are continuous except for well-developed substomatal chambers by which the stomata communicate with the internal leaf atmosphere.

The mesophyll includes equivalent, parallel, longitudinal veins, separated by assimilating layers which surround pseudolacunae. Each vein is supported by a well-developed parenchymatous and fibrous buttress, continuous with the hypodermis of each surface. Vascular tissues are quite complex but are not considered further in this account. The mesophyll between the veins is represented by large colourless cells which tend to be arranged in separate transverse plates. These cells collapse somewhat in mature leaves, so that in thin transverse sections there is an apparent lacuna between each adjacent pair of veins. These pseudolacunae are lined by small chlorenchyma cells, the adaxial layers often conspicuously palisade-like. The lacunae are also traversed by compact transverse diaphragms, mostly two cells thick. At frequent intervals these diaphragms include transverse vascular commissures which anastomose with the longitudinal veins. Strands of fibres, independent of the fibrous extensions of the bundle sheath, occur in a number of species, usually in the superficial layers.

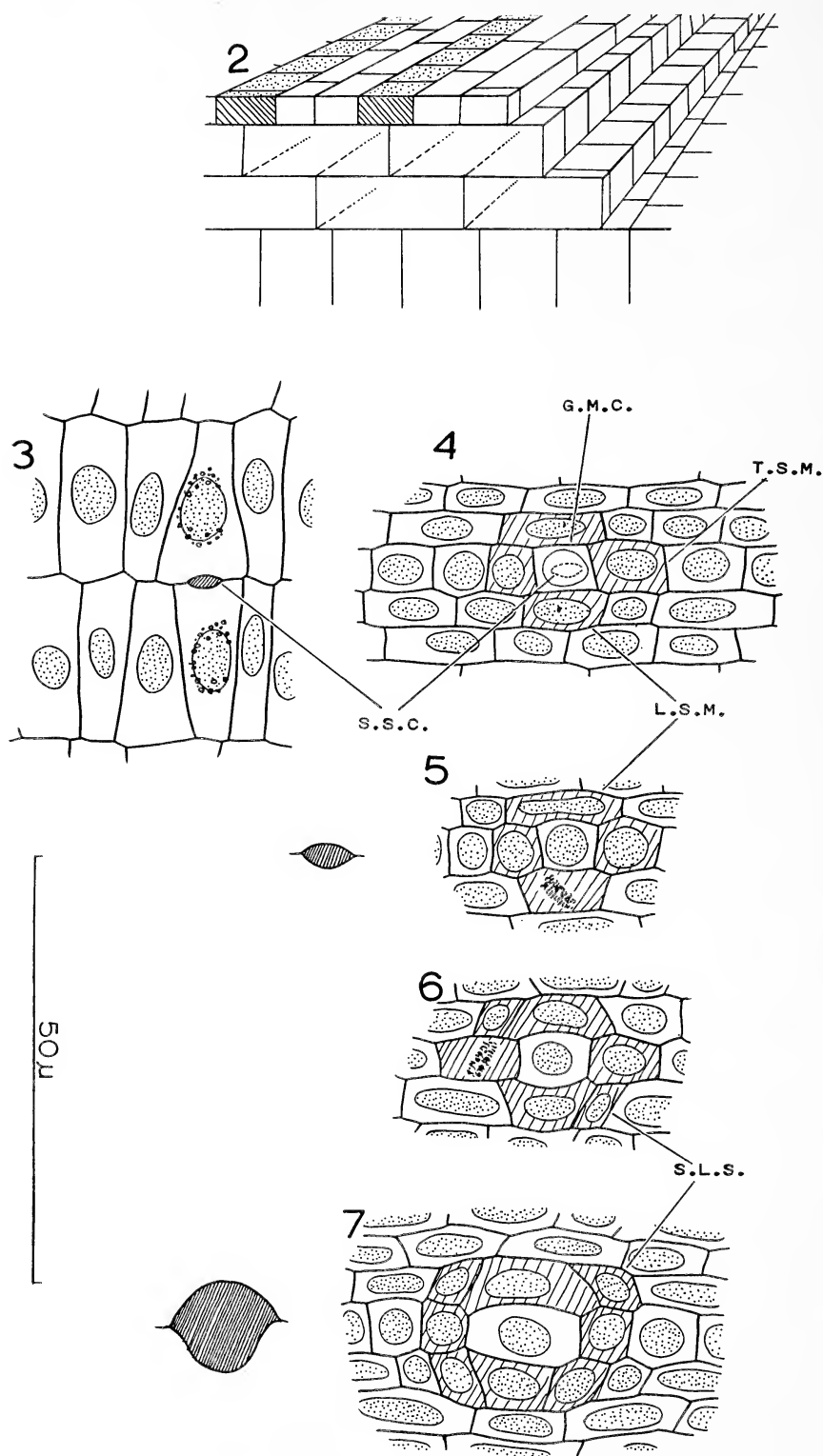
In the subsequent description an attempt has been made to employ a consistent terminology based on that used by Florin (1931). However,

Florin's terminology refers to gymnosperms. Stomata in Pandanaceae are tetracytic in the sense used by Metcalfe (1961). The cells next to the guard cells are subsidiary cells, of which there are four: two lateral subsidiary cells which are very different from normal epidermal cells, and two terminal (or polar) subsidiary cells which are less different from normal epidermal cells. The cells which immediately surround the subsidiary cells may be termed neighbouring cells, but the account of stomatal development below shows that neighbouring cells have different origins. They correspond approximately to the *Kranzzellen* of Florin, who uses the term "neighbouring cell" (*Nachbarzell*) collectively to signify any cell which surrounds the stomatal apparatus and differs from a normal epidermal cell. However, it is difficult to apply Florin's terminology strictly to Pandanaceae. Neighbouring cells in Pandanaceae vary in size and number and may or may not differ in varying degrees from normal epidermal cells.

#### STRUCTURE OF ABAXIAL STOMATA

Adaxial stomata are often different from abaxial stomata and are described briefly later.

Stomatal development has been described in *Pandanus graminifolius* by Pfitzer (1870) with an emphasis on the position of stomatal mother cells in relation to the hypodermal layers. Pfitzer's observations have been confirmed by my own study of stomatal development in four *Pandanus* species, using the method described by Stebbins and Khush (1961). Stomata always originate from epidermal cell files above the longitudinal anticlinal walls of the outermost hypodermal layer, but directly above the next innermost hypodermal layer (Fig. 2). Transverse divisions continue longest in future stomatal files, so their constituent cells are somewhat shorter, as well as wider, than cells in non-stomatal files. First evidence of stomatal differentiation occurs not in the epidermis itself but in the outermost hypodermal layer, by the development of substomatal chambers below future guard-cell mother cells (guard mother cells). Pfitzer emphasises this peculiarity and suggests that development of this internal cavity determines the presence of a stoma. The two hypodermal cells between which the chamber



originates (Fig. 3) are somewhat larger than adjacent hypodermal cells, have large nuclei, but most conspicuously include a fine granular deposit by which they may be recognized even before the chamber appears. Guard mother cells are recognizable by their position immediately above a chamber, but are not otherwise cytologically different from neighbouring cells of the stomatal file (Fig. 4). They only divide once after becoming recognizable, by the longitudinal wall which produces the guard cells, this usually being the last division in the development of the stomatal complex. Size of substomatal chamber gradually increases as the stomatal complex develops and is a useful indicator of the level of maturity of the complex (cf Figs. 5, 7).

Transverse divisions may continue in those cells of the stomatal file which are not guard mother cells. Such divisions in cells situated at each pole of the guard mother cell produce the terminal subsidiary cells (Fig. 6). These divisions are never synchronous and may occur early or late, but usually are completed before the divisions which delimit lateral subsidiary cells. Cells belonging to files on each side of the guard mother cell produce lateral subsidiary cells. Two successive divisions occur at opposite ends of each cell, each division cutting off by an oblique wall a small cell which is remote from the guard mother cell from a much larger cell next to the guard mother cell (Fig. 5). Rarely divisions in this lateral subsidiary mother cell are longitudinal and not oblique. The last division in the stomatal complex is almost invariably the longitudinal division which produces the guard cells, although rarely divisions producing terminal subsidiary cells do occur later than this.

Development of stomata does not follow a strict acropetal succession, and stomata at different stages of development occur in a small

area of the leaf. In general, however, divisions which produce terminal subsidiary cells are completed first; divisions producing lateral subsidiary cells, which occur throughout a relatively wide region, are completed second; and divisions which produce guard cells are usually last. Divisions within a single complex are rarely synchronous, so that only one division figure per stoma is usually seen.

Division in the guard-cell mother cell is associated with further internal development. As soon as guard cells are produced, but before the stomatal pore opens, enlargement of the substomatal chamber by separation within the second hypodermal layer occurs. When the stomatal pore opens there is thus communication with the internal leaf atmosphere.

This type of stoma corresponds to neither of the two main types recognized by Florin (1931) in gymnosperms, although it most resembles the amphicyclic. It is neither similar to development described by Stebbins and Khush in *Juncus* and *Sagittaria*, nor is it similar to that in *Tradescantia* as these authors suggest.

Because of the constant disposition of stomata in relation to the two outermost hypodermal layers and because of regular partitioning in these layers, the outer hypodermal cells which immediately surround the substomatal chambers have a very uniform shape and arrangement in all Pandanaceae. In the outermost layer the chamber represents a space between longitudinal walls and is enclosed by two U- or V-shaped cells (Fig. 20); in the next innermost layer the chamber represents a space between transverse walls and is surrounded by two kidney-shaped cells at right angles to the cells without (Fig. 21). Further inner hypodermal layers are not uniformly disposed. Variation in stomatal structure largely involves papillae developed on subsidiary and

FIGS. 2-7. Stomatal development in *Pandanus* ( $\times 1160$ ). 2, Diagrammatic representation of surface layers, showing epidermal stomatal files (stippled) in relation to hypodermal layers. 3, Arrangement of cells of outermost hypodermal layer at time of initiation of substomatal chamber. 4, Corresponding arrangement of epidermal cells immediately above Figure 3, stomatal complex recognized largely by position. 5, Oblique division in lateral subsidiary mother cell. 6, Transverse division in terminal subsidiary mother cell at a time when one division has occurred in each lateral subsidiary mother cell. 7, Arrangement of cells in stomatal complex prior to last division, that of the guard mother cell.

In Figures 4-7 the cells surrounding the guard mother cell are cross-hatched for ease of recognition. They are not distinguished in any obvious cytological way. Insert in Figures 5 and 7 shows size of corresponding substomatal chamber: s.s.c., substomatal chamber; g.m.c., guard mother cell; t.s.m., terminal subsidiary mother cell; l.s.m., lateral subsidiary mother cell; s.l.s., sister cell of lateral subsidiary cell.

neighbouring cells. Stomata which have no associated papillae represent the unspecialized state. A variety of types with gradually increasing elaboration of stomata can be recognized, culminating in stomata completely obscured by overarching papillae. In this continuous series a number of arbitrary types have been selected, each successive type representing an advance in specialization over the preceding one. However, a complete series of transitional types can be found connecting the arbitrary classes. *Pandanus* has the most variation. *Sararanga* has unspecialized stomata. *Freycinetia* forms rather a different class and is discussed separately.

(a) *Pandanus* and *Sararanga*

*Class 1: Unspecialized stomata* (Figs. 8–11, 19, 49–51). Each stoma has two guard cells, each guard cell more or less symmetrical in transverse view, with two equal cutinized ledges, each ledge situated above thickenings of the front wall (Figs. 9, 19). The cell lumen is wide and only slightly dumbbell-shaped in longitudinal view. Guard cells and lateral subsidiary cells are deeper than other epidermal cells, but not sunken. Lateral subsidiary cells are thin-walled and conspicuously different from normal epidermal cells. Terminal subsidiary cells are short but otherwise less well differentiated from normal epidermal cells (Fig. 8). Subsidiary and neighbouring cells are never elaborated, apart from slight overarching of lateral by terminal subsidiary cells. This type of stoma has been recorded in the following species:

*Sararanga*

*S. philippinensis*      *S. sinuosa*

The stomata in the two known species of *Sararanga* are therefore wholly unspecialized (Figs. 49–51).

*Pandanus*

*P. cominsii*      *P. pulposus*

*P. dubius*      *P. rockii*  
*P. odoratissimus* var. *P. tectorius*  
*laevis*      *P. veitchii*

Solla (1884) records them in:

*P. amarillifolius*      *P. pedunculatus*  
*P. cuspidatus*      *P. reflexus*  
*P. furcatus*      *P. stenophyllus*  
*P. javanicus*      *P. veitchii*

and in six unnamed species.

In subsequent stomatal classes, guard cells are identical in general structure, although they may vary considerably in size (cf Figs. 8, 10); an over-all range from 15–40  $\mu$  was observed in the material examined by me, corresponding closely to the range described by Solla.

*Class 2: Papillose lateral subsidiary cells* (Figs. 12–15). The construction described above is repeated, but with the addition of a row of 4–6 prominent papillae on the outer surface of each lateral subsidiary cell. There is no other stomatal elaboration, except for a tendency for terminal to overarch lateral subsidiary and guard cells to a greater extent than in Class 1 (Fig. 13). Degree of stomatal specialization commonly varies on a single leaf. For example, in material of *P. boninensis* and *P. odoratissimus* both Class 1 and Class 2 stomata were observed on the same leaf, together with intermediate stomata in which papillae occurred on one or another of the two lateral subsidiary cells belonging to a single stoma (Figs. 12, 14). A full row of papillae is always developed, never isolated or reduced numbers of papillae. Class 2 stomata have been observed in:

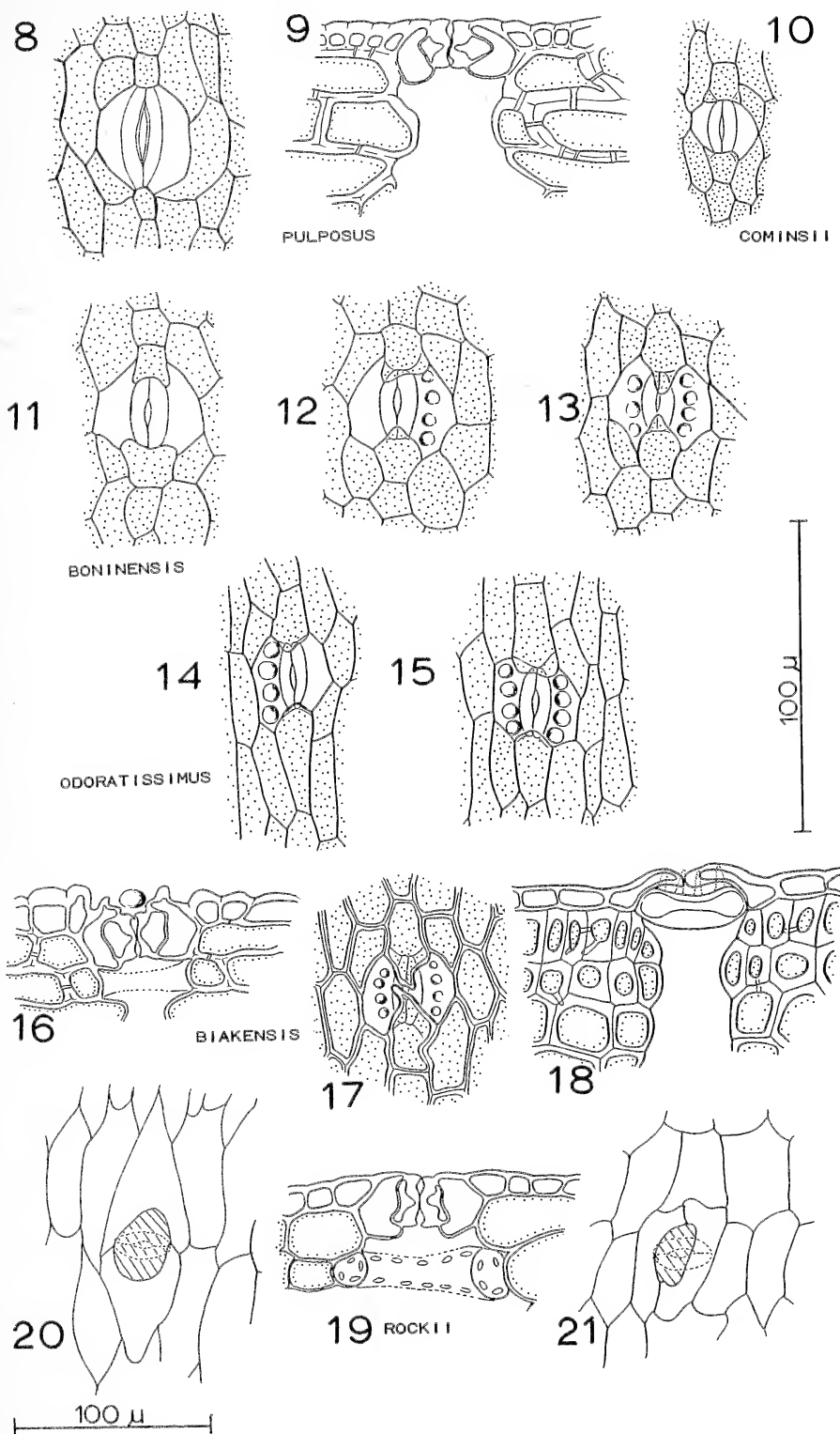
*P. baptistii*      *P. graminifolius* (Pfitzer)  
*P. boninensis*      *P. odoratissimus* var.

Solla records them for:

*P. furcatus*      *P. odoratissimus*  
*P. graminifolius*

and in two unnamed species.

FIGS. 8–21. *Pandanus*. Abaxial stomata classes 1 and 2 ( $\times 425$ , except 20 and 21, which are  $\times 270$ ). 8, 9, *P. pulposus*. 8, Surface view; 9, transverse section. 10, *P. cominsii*, surface view; guard cells are among the shortest in the genus. 11–13, *P. boninensis*, different types of stomata from same area of single leaf. 14, 15, *P. odoratissimus*, different types of stomata from same area of a single leaf. 16–18, *P. biakensis*. 16, Transverse section; 17, surface view; 18, longitudinal section. 19–21, *P. rockii*. 19, Transverse section; 20, 21, arrangement of hypodermal cells around substomatal chambers; 20, outermost hypodermal layer; 21, next innermost layer.



The stomata in *P. boninensis* and *P. graminifolius* are somewhat transitional to the next category.

In all subsequent stomatal classes, papillae on lateral subsidiary cells are developed in exactly the same way, together with other kinds of papillae on other cells. However, the former kind of papillae always remains simple, regardless of elaboration in the latter kind of papillae. Their only variation is in height, taller papillae being up to 25  $\mu$  high, as in *P. aurantiacus*.

*Class 3: Papillose terminal and lateral subsidiary cells* (Figs. 16–18). The slight tendency in Class 2 stomata for the terminal to protrude over the lateral subsidiary cells is much more pronounced in Class 3. This is associated with a tendency for the guard and lateral subsidiary cells to be sunken within the epidermis. Each of the terminal subsidiary cells then has a prominent papilla which overarches the stomatal pore. Frequently papillae from opposite poles meet and overlap, their ends being mutually displaced (Fig. 17), or the papillae may even fork to produce short interdigitating branches. Such papillae are usually adpressed closely to the stomatal pore, between the opposite files of papillae born by lateral subsidiary cells (Fig. 18). Species within this category include:

*P. biakensis*   *P. copelandii*   *P. furcatus*

*Pandanus biakensis* approaches the following type.

*Class 4: Papillose neighbouring and subsidiary cells* (Figs. 22–33). An advance on Class 3 is represented by the development of papillae which protrude from neighbouring epidermal cells. This augments the outer stomatal cavity produced by sinking of the stomatal apparatus in the epidermis. The relation between papillae associated with stomata and those elsewhere on the epidermis is discussed later. Class 4 stomata are very diverse because the size and frequency of this new kind of papilla varies considerably. In the less elaborate types papillae are not pronounced, as in *P. douglassii* (Figs. 22–24), so that the outer chamber is shallow, but in more

elaborate types the papillae are very tall and form a distinct "stockade" surrounding a very deep outer chamber, as in *P. utilis* (Figs. 28–30). Tall papillae further show a marked tendency to overarch and occlude the outer chamber (e.g., *P. parkinsonii*, Figs. 25–27).

Papillae themselves are diverse. They may form as a result of protrusion of the whole outer wall of the epidermal cell, or involve only part of the outer wall. Less commonly, several papillae may arise from each epidermal cell, as in *P. patina* (Fig. 32). Finally, the more elaborate members of this class show a tendency for the papillae surrounding the stomata to become lobed or shortly branched. Usually this is noticeable first in the terminal subsidiary cells, as in *P. utilis* (Fig. 30), and in this way a transition to Class 5 occurs. In *P. candelabrum* the papillae are very low but often distinctly lobed.

The following species have been included in Class 4, although it is clear from Figures 22–30 that the assemblage is heterogeneous:

<i>P. aimiriikensis</i>	<i>P. parkinsonii</i>
<i>P. candelabrum</i>	<i>P. patina</i>
<i>P. douglassii</i>	<i>P. pistillatus</i>
<i>P. heterocarpus</i>	<i>P. utilis</i>
<i>P. microcarpus</i>	<i>P. whitmeeanus</i>
<i>P. nemoralis</i>	

Solla records elaborate stomata in the following species, without making distinction between classes 4 and 5 in the way I have done:

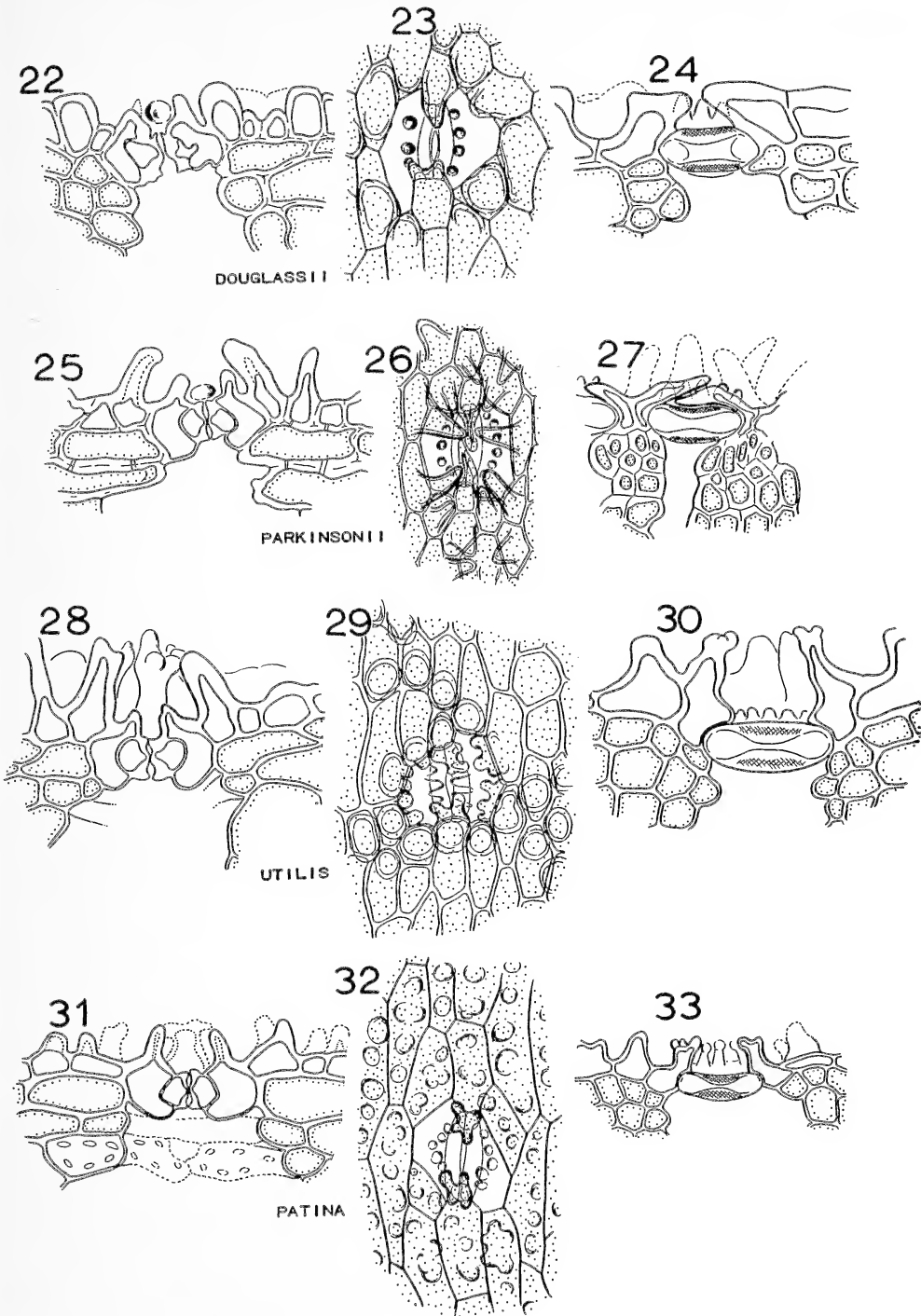
<i>P. caricosus</i>	<i>P. silvestris</i>
<i>P. helicopus</i>	<i>P. tenuifolius</i>
<i>P. microcarpus</i>	<i>P. utilis</i>
<i>P. odoratissimus</i>	

and in 13 unnamed species.

*Class 5: Overarching papillae lobed or dendritic* (Figs. 34–45). This class includes the most specialized forms. Sinking of the stomata is pronounced, the deep outer stomatal chamber so formed being partly or wholly occluded by the branched papillae of terminal subsidiary and neighbouring cells. In the least elaborate members papillae are short and little lobed, as in *P.*

FIGS. 22–33. *Pandanus* abaxial stomata of classes 3 and 4. 22–24, *P. douglassii*. 22, Transverse section; 23, surface view; 24, longitudinal section. 25–27, *P. parkinsonii*. 25, Transverse section; 26, surface view; 27, longitudinal section. 28–30, *P. utilis*. 28, Transverse section; 29, surface view; 30, longitudinal section. 31–33, *P. patina*. 31, Transverse section; 32, surface view; 33, longitudinal section.





100  $\mu$

*capitellatus*, which is thus intermediate between classes 4 and 5 (Figs. 34–36). Increasing elaboration can be seen in a number of species whereby the papillae become taller, elaborately lobed distally, the lobes tending to interdigitate and form an incomplete canopy above the outer stomatal chamber (Figs. 40–45). The ultimate condition, and the most elaborate stomatal type in *Pandanus*, was observed in an unidentified species cultivated in Florida in which the canopy was so complete that the guard cells were completely obscured from surface view, a somewhat more elaborate condition than that illustrated in Figure 44.

As in previous classes the papillae arising from terminal subsidiary cells may be either erect or adpressed to the pore (Fig. 42), a feature constant for each species. Where these papillae are adpressed, and indeed to a certain extent in other examples, the outer chamber is partially occluded by papillae which are elevated to three different levels: papillae from the lateral subsidiary cells being shortest, from the terminal subsidiary cells being intermediate, and from the neighbouring cells being tallest (Figs. 40, 43). Clearly, in these most elaborate types water vapour must pass through quite a labyrinth on its way through the epidermis. Species of this category include:

<i>P. archboldianus</i>	<i>P. erinaceus</i>
<i>P. aurantiacus</i>	<i>P. nigridentis</i>
<i>P. capitellatus</i>	<i>P. pygmaeus</i>

(b) *Freycinetia*

*Freycinetia* includes species with unspecialized stomata, corresponding to Class 1 above, and where stomatal elaboration does occur it seems to follow a different trend to that in *Pandanus*, although insufficient material has been examined to be certain of this point. Specialization in *Freycinetia* involves sunken stomata, overarched by simple papillae from terminal and neighbouring cells only. Papillae are never lobed. Rows of papillae on lateral subsidiary cells which are so

characteristic of stomata in classes 2–5 in *Pandanus* have never been observed in *Freycinetia*, except by Solla in one unnamed species (which might be a *Pandanus* misidentified). Further observation is needed to discover if there is a constant difference between *Pandanus* and *Freycinetia* in this respect. Figures 46–48 represent the most elaborate condition seen by me in *Freycinetia*.

The following species, together with six unnamed species listed by Solla, have unspecialized stomata:

<i>F. banksii</i>	<i>F. lucens</i>
<i>F. excelsa</i>	<i>F. mariannensis</i>
<i>F. javanica</i>	

The following has specialized stomata:

*F. arborea*

Solla records specialized stomata in three unnamed species.

Further peculiarities of epidermal structure in *Freycinetia* are mentioned below.

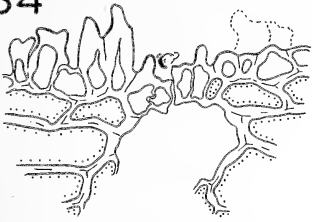
#### VARIATION IN STOMATAL STRUCTURE

The above account gives an impression of the range of stomatal structure throughout the Pandanaceae and, at least for *Pandanus*, demonstrates a linear series of increasingly specialized types, each arbitrary class which has been distinguished being more specialized than the preceding. This trend seems to be unidirectional, as can be understood when the stomatal variation in a single individual is considered. A number of ancillary observations need to be outlined first.

(i) *Occluded stomata*. Frequently stomata were observed which stain intensively with safranin, in contrast to normal stomata. These evidently correspond to the "lignified" stomata of Köfler (1918). Such stomata become occluded by resinous or tanniferous material which plugs the stomatal pore. Subsequently the guard cells die and their back walls collapse against the front walls. Usually the substomatal

FIGS. 34–45. *Pandanus* abaxial stomata of classes 4 and 5 (except 39, which shows an adaxial stoma). 34–36, *P. capitellatus*. 34, Transverse section; 35, surface view; 36, longitudinal section. 37, 38, *P. pygmaeus*. 37, Transverse section; 38, surface view. 39–42, *P. archboldianus*. 39, Adaxial stoma, surface view; 40, transverse section; 41, surface view; 42, longitudinal section. 43–45, *P. nigridentis*. 43, Transverse section; 44, surface view; 45, longitudinal section.

34

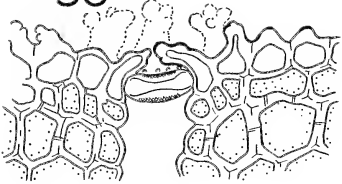


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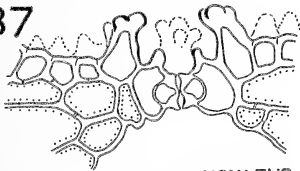


CAPITELLATUS

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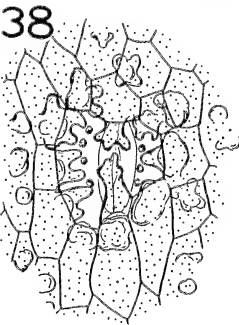


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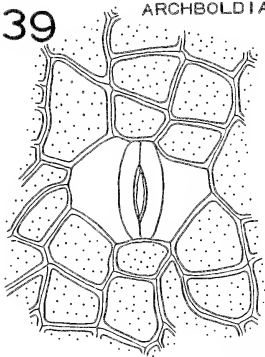


PYGMÆUS

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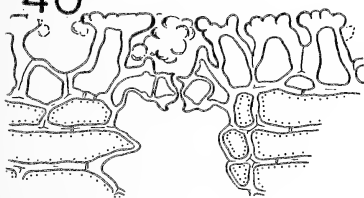


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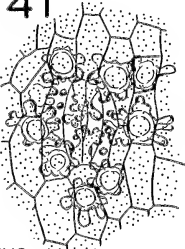


ARCHBOLDIANUS

40

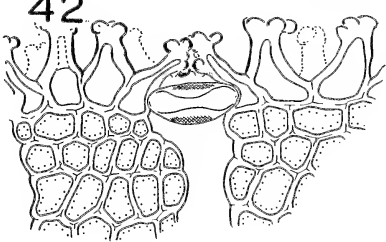


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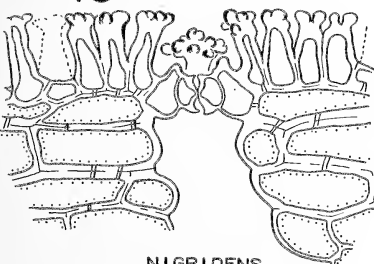


ARCHBOLDIANUS

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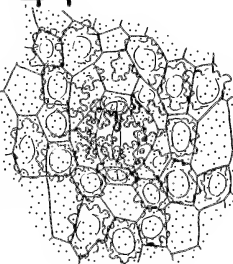


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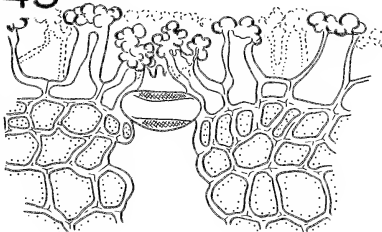


NIGRIDENS

44



45



100  $\mu$

hypodermal cells put out tylose-like protuberances which fill the substomatal chamber. These invaginations may eventually become thick-walled and pitted. Positive lignin reactions by which Köfler recognized these stomata are apparently a property of the resinous material which initiates these changes, although walls of hypertrophied hypodermal cells may subsequently become lignified. Such occluded stomata are very irregular in their distribution, often being localized. I have observed them in most species examined, although Köfler lists a number of species in which they were not observed. This is probably not significant taxonomically, since the potentiality for their development in old leaves possibly exists in all species. Whether they are pathological or not is not known.

(ii) *Variation within a single leaf.* Discussion of epidermal papillosity has so far dealt only with cells next to stomata. Papillae are sometimes restricted to cells in the vicinity of stomata, as in *P. candelabrum* and *P. whitmeeanus*, but are more usually distributed, either uniformly or nonuniformly, over the whole abaxial epidermis. Papillae associated with stomata are usually taller than those elsewhere. When they are uniformly distributed papillae occur equally in costal and intercostal regions, although costal are almost invariably lower than intercostal papillae and are equally developed on all cells (e.g., *P. erinaceus* and *P. patina*). Otherwise they are restricted to intercostal regions. A striking and not infrequent condition is for epidermal papillae to be restricted so that they form a distinct reticulum in surface view, with strands of the "network" meeting about the stomata (e.g., *P. capitellatus* and *P. utilis*, Fig. 29). In general, specialisation of epidermal papillae closely parallels specialisation of stomata, although anomalous instances where it does not are described below.

Stomata are very constant in structure throughout a single leaf surface, but adaxial may differ strikingly from abaxial. Adaxial stomata vary in number but are always fewer than abaxial. They are always unspecialized and never appreciably sunken, even in species with very elaborate abaxial stomata. Consequently, in these species the difference between adaxial and abaxial stomata is very striking (cf Figs. 39, 41).

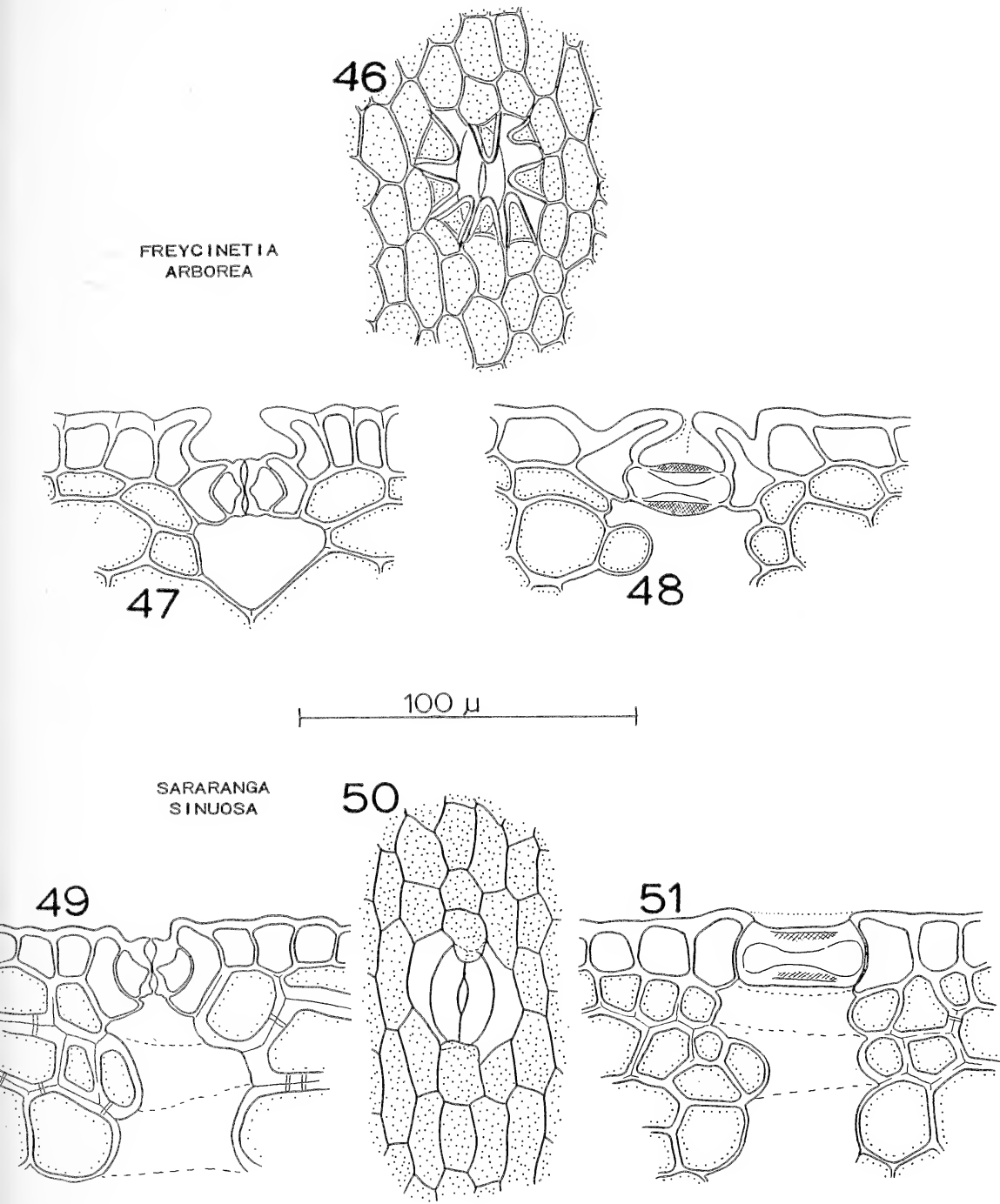
(iii) *Variation throughout a single individ-*

*ual.* The trend in stomatal elaboration demonstrated throughout *Pandanus* is partly or wholly demonstrated by a single individual in many species. This is because seedling leaves and the first leaves on each renewal branch of the sympodium always possess unspecialized stomata. Thereafter, on subsequent transitional leaves or scale leaves there is a gradual increase in stomatal elaboration culminating in stomata of maximum elaboration developed by a particular species. This maximal condition appears first on the first true foliage (or adult) leaves of a shoot (Fig. 1). Thus on a shoot capable of developing elaborate stomata, a long transitional series of stomatal types can be demonstrated in the scale-leaf series; otherwise, where the species does not develop specialized stomata the range of types on a single shoot may be limited, or there may be only one type. This concept is illustrated diagrammatically in Figure 52. From this it is evident that each species of *Pandanus* has a maximum potential for stomatal elaboration which is achieved gradually on each new shoot. In some species (those which bear Class 5 stomata) the potential is great; in others (those which bear lower class stomata) the potential is limited. Many species have no potential for stomatal elaboration. That this maximum potential is always fully expressed on adult foliage leaves is clear from examination of many samples of a single species from different sources. Thus *P. utilis* always has stomata of the type illustrated in Figures 28–30 on its adult foliage.

Associated with the frequent increase in stomatal complexity on successive leaves of a single shoot is an increase in stomatal number. Prophylls always have very diffusely distributed stomata, in successive scale leaves they become dense, and a more or less constant value is achieved in normal foliage leaves. This is a genuine increase in stomatal index, since epidermal cell size is quite uniform throughout this range of leaf types.

The pattern of stomatal variation described above is familiar in many other plants (e.g., gymnosperms; Florin, 1931). It is easy to demonstrate in *Pandanus* because of the relatively simple linear sequence of increasing stomatal complexity and the constancy of shoot construction which makes leaf categories easy to recognize (Figs. 1, 52).

The patterns of variability in stomata have



FIGS. 46–51. *Freycinetia* and *Sararanga*, abaxial stomata ( $\times 425$ ). 46–48, *Freycinetia arborea*. 46, Surface view; 47, transverse section; 48, longitudinal section. 49–51, *Sararanga sinuosa*. 49, Transverse section; 50, surface view; 51, longitudinal section.

been described in such a way as to suggest that development of papillae on epidermal cells remote from stomata closely parallels that on cells immediately associated with stomata. This is undoubtedly true for most *Pandanus* species, but there is evidence in *Freycinetia excelsa* and in an unnamed species of *Pandanus* cultivated in Florida that epidermal papillae may proliferate quite independently of stomata. In the former example some shoots had leaves with a distinctly papillose abaxial epidermis, although the stomata remained quite unspecialized. Clearly, there may be independence between epidermal and stomatal papillae in some Pandanaceae, and my account with the emphasis on a linear correlation between the two does not tell the whole story.

DISCUSSION

Patterns of anatomical features in the leaf which are of diagnostic value have not yet

been demonstrated in the Pandanaceae. Stomatal structure, which shows most variation, must be used cautiously for systematic purposes in view of its variation in a single individual. So far there is little indication that stomatal type is taxonomically significant.

Stomata in Pandanaceae vary in a way which might suggest a relation with environmental aridity. It is clear, however, that the degree of stomatal elaboration is under genetic control and is not wholly a consequence of external environment. Evidence is provided by a number of species of *Pandanus* cultivated side by side under identical circumstances in Florida. In this collection the whole range of stomatal types in Classes 1–5 has been seen, so that in this collection the release of stomatal potential is not affected by environment. Conversely, material of *P. dubius* from contrasted environments, supplied by Dr. B. C. Stone, showed no variation in stomatal elaboration.

If it is probable that stomatal elaboration is

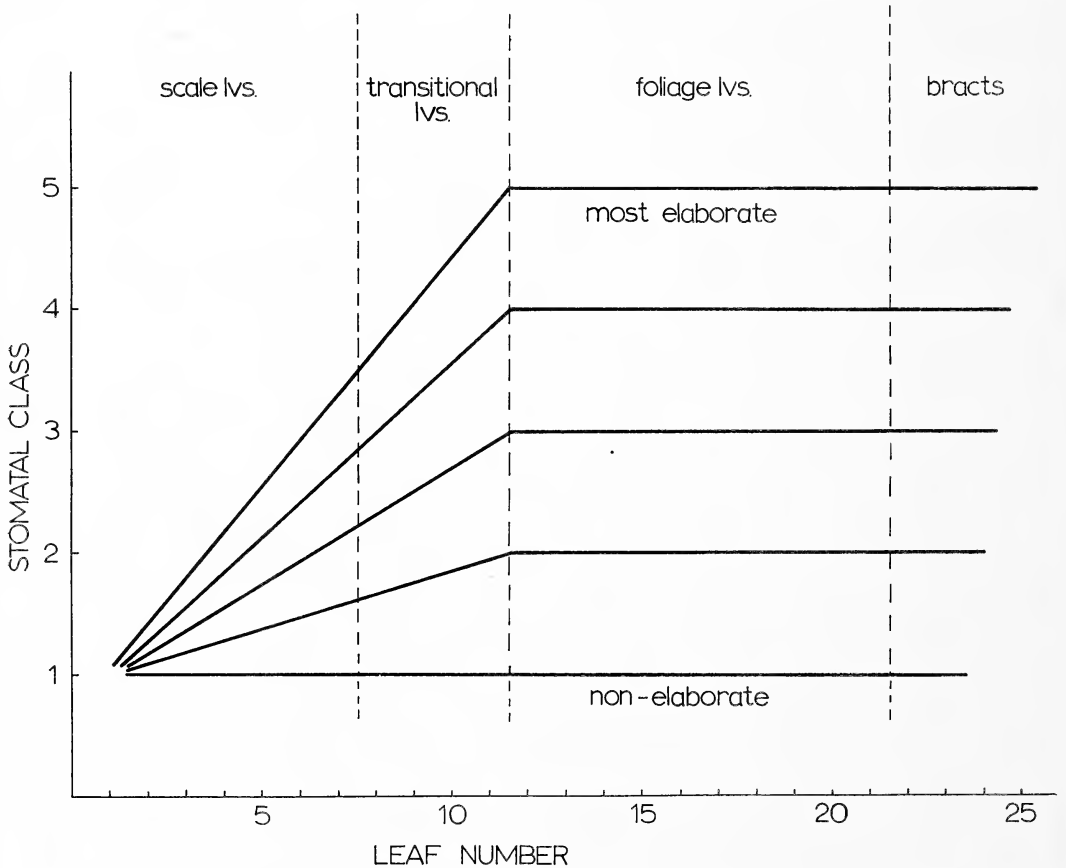


FIG. 52. Diagram representing increasing elaboration of stomata on a single shoot, the ultimate potential differing in different species (cf Fig. 1).

differently expressed in closely related species, it is possible that elaboration is an ecological adaptation which has become fixed genetically. It is an attractive hypothesis to regard elaborate epidermal structures associated in varying degrees with the guard cells as devices whereby transpiration is reduced, since this type of modification is frequent in plants of dry regions. However, in *Pandanus* an increase in epidermal papillosity does not involve a comparable increase in cuticular thickness. Therefore elaborate papillae actually increase surface area and presumably also cuticular transpiration. There may be overcompensation for this by reduction in stomatal transpiration through obstruction of the outer stomatal chamber. A more obvious antitranspiration device is the plugging of many stomata (the "lignified" stomata of Köfler) by resinous deposits, although this mechanism seems irregular.

Stomatal elaboration might therefore be interpreted more readily in terms of ecology and physiology than of taxonomy. *Pandanus* occupies a wide range of habitats (van Steenis, 1956) and it would be valuable to examine stomatal structure of species occupying contrasted habitats. Also the basic physiology of water conduction in *Pandanus* is itself relevant. *Pandanus* has vessel elements with scalariform perforation plates bearing many thickening bars in all parts, elements of the root being somewhat more specialized than those of the leaf and stem. Even if the stem is an efficient water conductor, it is likely to be subject to water stress as it grows older. The leafy crown tends to increase in size by branching, but the main axis, being devoid of a secondary vascular cambium (Schoute, 1907), has no means of increasing the volume of water conducting tissue (Tomlinson, 1964). Reduction of water lost through the leaf surface would evidently be favourable, regardless of the environment.

No one single factor, therefore, can explain stomatal elaboration in Pandanaceae, since it may be correlated partly or wholly with several unrelated factors, notably phylogeny, ecology, and physiology, together with over-all stature and growth form. The limited scope of the present study should now be quite clear, as well as the enormous scope for future observation.

MATERIAL EXAMINED

*Pandanus*

(i) Dried specimens from Bishop Museum, Honolulu

<i>P. aimiriikensis</i> Martelli.....	St. John 25884
<i>P. archboldianus</i> Merr. and Perry .....	Barrett 10203
<i>P. biakensis</i> St. John.....	St. John 26142
<i>P. boninensis</i> Warb.....	Fosberg 31483
<i>P. capitellatus</i> Merr. and Perry .....	Stone 2466
<i>P. cominsii</i> Hemsl.....	Stone 2549
<i>P. douglassii</i> Gaud.....	Pearsall 74
<i>P. dubius</i> Spreng.....	St. John 25898
<i>P. erinaceus</i> B. C. Stone.....	Stone 2578
<i>P. nemoralis</i> Merr. and Perry.....	Stone 2483
<i>P. nigridens</i> B. C. Stone.....	Stone 2539
<i>P. odoratissimus</i> L.f. var.....	Doty 16791
<i>P. parkinsonii</i> Martelli.....	Stone 2615
<i>P. pistillatus</i> Martelli.....	Stone 2576
<i>P. pulposus</i> (Warb.) Martelli .....	Stone 1110
<i>P. whitmeeanus</i> Martelli.....	Stone 2209

(ii) Other sources

Cultivated in Florida:

<i>P. baptistii</i> Hort.
<i>P. copelandii</i> Hort.
<i>P. utilis</i> Bory

Cultivated at Foster Botanic Garden, Honolulu, Hawaii:

<i>P. odoratissimus</i> L.f. var. <i>laevis</i>
<i>P. patina</i> Martelli
<i>P. c.f. pygmaeus</i> Thou.
<i>P. rockii</i> Martelli
<i>P. sp.</i> ("Hala")

Slide collection, Jodrell Laboratory, Royal Botanic Gardens, Kew:

<i>P. aurantiacus</i> Ridl.
<i>P. furcatus</i> Roxb.
<i>P. heterocarpus</i> Balf.
<i>P. microcarpus</i> Balf.
<i>P. tectorius</i> Sol.
<i>P. utilis</i> Bory

Slide collection, Professor V. I. Cheadle, at University of California, Davis, California:

<i>P. utilis</i> Bory.....	Atkins Garden, Cienfuegos, Cuba
<i>P. veitchii</i> Hort.....	Atkins Garden, Cienfuegos, Cuba

## Collections from wild:

*P. candelabrum* Beauv.....Akofokyir,  
Cape Coast, Ghana

*Freycinetia*

## Collections from wild:

*F. arborea* Gaud.....Poamoho Trail,  
Oahu, Hawaii

*F. mariannensis* Mert...Stone 4217, Guam  
Slide collection, Jodrell Laboratory, Royal  
Botanic Gardens, Kew:

*F. banksii* Cunn.

*F. javanica* Bl.

*F. lucens* Ridl.

Slide collection, Professor V. I. Cheadle, at  
University of California, Davis, California:

*F. excelsa* F. Muell.....CA. 216 and 230  
Atherton and Cairns, Australia

*Sararanga*

Dried specimen from Herbarium, Royal  
Botanic Gardens, Kew:

*S. philippinensis* Merr.....Ramos and  
Edaño 48047, Philippines

## Collection from wild:

*S. sinuosa* Hemsl.....G. F. C. Dennis 340,  
British Solomon Islands

## ACKNOWLEDGMENTS

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<sup>2</sup> It is hoped to describe in detail the anatomy of *Sararanga* in a future account based on Mr. Dennis's collections.



# New Monogenetic Trematodes from Hawaiian Fishes, I<sup>1</sup>

SATYU YAMAGUTI

THE PRESENT REPORT is based on the collections made by my technical assistant, Mr. Shunya Kamegai, in 1963. The source of material was chiefly from the Honolulu Fish Market, and partly from the University Aquarium at Waikiki Beach. I am particularly indebted to the director of the Aquarium, Prof. S. W. Tinker, for his supply of frozen fish material from which my first collections of monogenetic forms were made. I wish to express my appreciation also to Prof. W. A. Gosline, Department of Zoology, University of Hawaii, who identified the fish; Prof. G. W. Chu, Department of Microbiology, for his official sponsorship on behalf of the University of Hawaii; Mr. S. Kamegai for collecting parasites and drafting the figures of the parasites; and Mrs. S. Yamaguti for finishing the figures, preparing the plates, and typing the manuscript.

The monogenetic trematodes of the Hawaiian fishes have so far remained unexplored, so that special attention was directed to this group of trematodes. It is surprising that Hawaiian fishes are very commonly infested with monogenetic trematodes and that the parasites so far examined are all, with some exceptions, new to science. It will take, therefore, a long series of years to report all the findings. For this reason I have decided to report here only those new species representing new genera, before describing the large numbers of species which remain to be published in a later monograph. Some of the new genera represent new subfamilies, or even new families, as indicated in the list given below. The holotype specimens and some of the paratypes mounted on the same slides as the holotype will be deposited in the Helminthological Collection of the United States National Museum at Beltsville, Maryland, and the paratypes will be deposited along with described species in the Meguro Parasitological Museum in

Meguro, Tokyo, where I shall be in active research service after completing my research project in the United States.

The new genera described below are assigned to different families as follows:

## I. CAPSALIDAE Baird, 1853

Benedeniinae Johnston, 1931

1. *Dioncopsseudobenedenia kala* n. g., n. sp.
  2. *Oligoncobenedenia nasonis* n. g., n. sp.
- Pseudonitzschiinae n. subf.
3. *Pseudonitzschia uku* n. g., n. sp.

## II. MONOCOTYLIDAE Taschenberg, 1879

Monocotylinae Gamble, 1896

4. *Diplobheterocotyla dasyatis* n. g., n. sp.

## III. DACTYLOGYRIDAE Bychowsky, 1933

Ancyrocephalinae Bychowsky, 1937

5. *Neohaliotrema maomao* n. g., n. sp.
6. *Pseudempleurosoma carangis* n. g., n. sp.

## IV. DIPLECTANIDAE Bychowsky, 1957

7. *Nasobranchitrema pacificum* n. g., n. sp.

## V. PSEUDODICLIDOPHORIDAE n. fam.

Pseudodiclidophorinae n. subf.

8. *Pseudodiclidophora decapтери* n. g., n. sp.
- Allopseudodiclidophorinae n. subf.
9. *Allopseudodiclidophora opelu* n. g., n. sp.

## VI. DISCOCOTYLIDAE Price, 1936

Opisthogyninae Unnithan, 1962

10. *Pseudopisthogyne lepidocybii* n. g., n. sp.
11. *Allopseudopisthogyne constricta* n. g., n. sp.
12. *Pseudopisthogyneopsis lepidocybii* n. g., n. sp.

Pseudodiscocotylinae n. subf.

13. *Pseudodiscocotyla opakapaka* n. g., n. sp.

<sup>1</sup> Contribution from Department of Microbiology, University of Hawaii, supported by a grant (GB-78) from the National Science Foundation. Manuscript received April 25, 1963.

## VII. AXINIDAE Unnithan, 1957

Allopseudaxininae Yamaguti, 1963

14. *Allopseudaxinoides euthynni* n. g., n. sp.

Monaxininae Unnithan, 1957

15. *Allomonaxine carangoides* n. g., n. sp.

## VIII. GASTROCOTYLIDAE Price, 1943

Gastrocotylinae Sproston, 1946

16. *Pseudochaubanea sphyraenae* n. g., n. sp.

Areotestiinae n. subf.

17. *Areotestis sibi* n. g., n. sp.

## IX. ALLOMICROCOTYLIDAE n. fam.

18. *Allomicrocotyla onaga* n. g., n. sp.

1. *Dioncopseudobenedenia kala* n. g., n. sp.

Fig. 1

HABITAT: Gill of *Naso unicornis*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y.

No. 1.

DESCRIPTION (based on 18 whole mounts): Body flattened, oval or more elongate, 2.1–4.2 mm in length, with maximum width of 0.6–2.0 mm in middle third; cuticle beset with conical papillae. Opisthohaptor circular 0.5–1.0 mm in diameter, aseptate, fringed with scalloped membrane up to 25 $\mu$  wide, provided with only one pair of slender, rather acicular spines 50–75 $\mu$  long behind the center, where the haptor is attached dorsally to the body proper by a short muscular stalk; spines usually straight, apparently no more functional. Prohaptor suckorial, 0.16–0.3 mm in longer diameter, with strongly muscular wall, the anterolateral part of which contains granular, apparently glandular tissue; the two suckers are connected by a flat apical border of the body proper. Two pairs of compact eye-spots anterodorsal to pharynx. Mouth followed by a distinct prepharynx which consists of circular muscle lamellae and provided inside with more or less prominent cuticular papillae, measuring 0.1–0.24  $\times$  0.14–0.3 mm. Pharynx subglobular, 0.14–0.34  $\times$  0.16–0.38 mm, consisting mainly of radial muscle fibers enclosed in smooth capsule of circular muscle fibers. Intestinal limbs with numerous subdivided outer branches and fewer short inner branches, not confluent posteriorly; outer branches with longi-

tudinal anastomosis parallel to principal limb.

Testes oval, 0.2–0.5  $\times$  0.15–0.38 mm, directly juxtaposed, just pre-equatorial. Paired Goto's gland irregular in shape and size, containing a variable number of rounded nuclei and fine granules; the nuclei are massed together and pressed to one side of the gland or to the posterior end, sometimes showing signs of degeneration; the granules, when liquefied, occupy some or greater part of the cell. In the type the vas deferens contains a small oval degenerating nucleus in addition to spermatozoa at its very beginning among the ovary and testes; this obviously originated from the Goto's gland. After convolutions in front of the vitelline reservoir the vas deferens crosses over the uterus dorsally and penetrates the cirrus pouch near its posterior end; ejaculatory duct well provided with circular muscles, joining with prostatic duct at base of cirrus. Cirrus pouch claviform, 0.36–0.95  $\times$  0.08–0.22 mm, with thick wall of circular muscle fibers, containing prostatic reservoir 0.13–0.33 mm long by 0.05–0.28 mm wide at base, occupied for greater part by muscular ejac-

## ABBREVIATIONS USED IN FIGURES

Ac	Accompanying cell	GT	Gonotyl
ACO	Accessory copulatory organ	HG	Head gland
ACS	Accessory copulatory sclerite	HO	Head organ
AG	Apical gland	M	Mouth
AO	Apical organ	O	Ovary
AR	Atrial ring	OC	Eye spot
AS	Atrial spine	OS	Oral sucker
AVD	Anterior vitelline duct	P	Pharynx
AVGD	Accessory vaginal duct	PC	Prostatic cell
BC	Bulbus cirri	PD	Prostatic duct
BE	Bulbus ejaculatorius	PL	Preoral lobe
C	Cirrus	PM	Pars muscosa
CP	Cirrus pouch	PP	Pars prostatica
DE	Ductus ejaculatorius	PR	Prostatic reservoir
E	Egg	RS	Receptaculum seminis
ES	Esophagus	S	Sucker
EV	Excretory vesicle	SP	Sphincter
GA	Genital atrium	SV	Seminal vesicle
GI	Genito-intestinal canal	T	Testis
GO	Goto's organ or gland	V	Vagina
GP	Genital pore	VC	Vitelline commissure
		VD	Vas deferens
		VP	Vaginal pore
		VR	Vitelline reservoir
		VT	Vitelline gland
		VTD	Vitelline duct
		*	Seminoprostatic reservoir

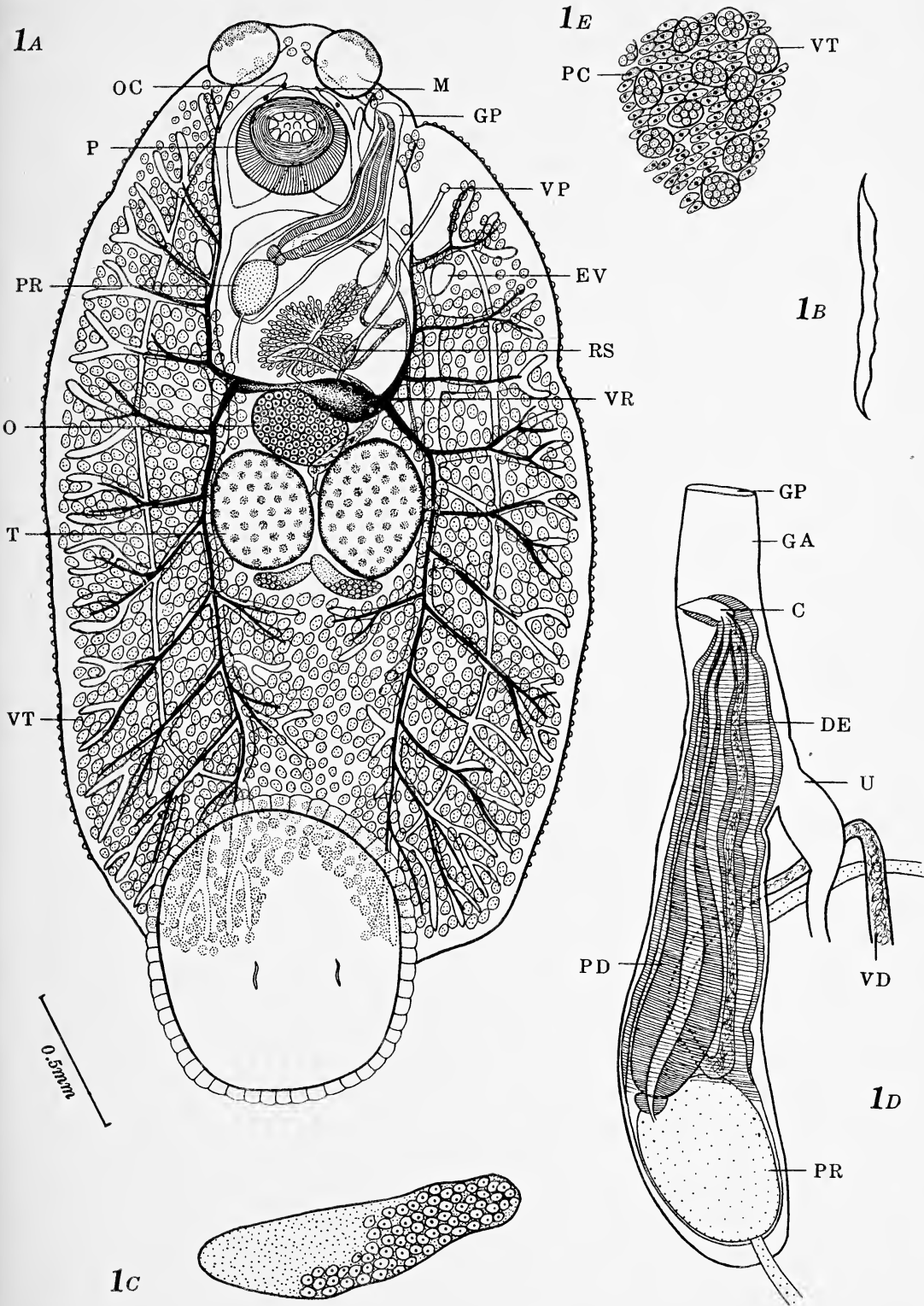


FIG. 1. *Dioncopseudobenedenia kala* n. g., n. sp. 1A, Holotype, ventral view; 1B, haptor with spine; 1C, Goto's gland; 1D, terminal genitalia, ventral view; 1E, prostate cells extensively developed among vitelline follicles.

ulatory duct and prostatic duct with thick wall of circular muscle fibers. Prostatic duct may or may not be provided proximally with a small sphincter-like bulb. Prostate cells extensively developed among vitelline follicles. Cirrus conical, unarmed, muscular, 10–15 $\mu$  long. Genital atrium thin-walled, apparently extending inwards down to the point where the uterus opens into it. Genital pore immediately posterolateral to left prohaptor.

Ovary subglobular to oval, 0.07–0.23  $\times$  0.09–0.32 mm; ootype medial to vas deferens curve; eggs about 120  $\times$  80 $\mu$ , with long filament. Uterus opening into genital atrium at a distance of about 0.3 mm from genital pore in the type. Vagina opening dorsally posterolateral to genital pore; vaginal duct crossing vas deferens coils ventrally and forming elongate seminal receptacle 50 $\mu$  wide in the type, latter opening into vitelline reservoir by a short narrow duct. Vitellaria co-extensive with intestinal branches; vitelline reservoir anterosinistral to ovary, 0.04–0.17  $\times$  0.05–0.3 mm.

DISCUSSION: This genus resembles *Pseudobenedenia* Johnston, 1931, in internal anatomy, especially in that the prostatic reservoir is enclosed in the cirrus pouch, but differs from it in possessing only one pair of rudimentary anchors instead of three pairs, and in the extensive development of prostate cells among the vitelline follicles.

#### *Dioncopsudobenedenia* n. g.

GENERIC DIAGNOSIS: Capsalidae, Benedeniinae. Prohaptor sucker-like, partly with glandular tissue. Opisthohaptor disclike, aseptate, with scalloped marginal membrane and only one pair of spines or anchors. Eyes present. Pharynx muscular or glandular. Intestinal limbs with inner and outer branches, not confluent posteriorly; outer branches united by longitudinal anastomosis parallel to principal limb. Testes juxtaposed, entire. Vas deferens winding in front of vitelline reservoir. Prostatic reservoir enclosed in cirrus pouch; prostate cells extensively developed among vitelline follicles. Common genital pore marginal or submarginal, immediately behind left prohaptor. Ovary entire, immediately pretesticular. Eggs filamented. Vagina with sub-

marginal dorsal opening near genital pore. Vitelline reservoir anterosinistral to ovary. Parasitic on gills of marine teleosts.

TYPE SPECIES: *D. kala* n. sp., on *Naso unicornis*; Hawaii.

#### 2. *Oligoncobenedenia nasonis* n. g., n. sp.

Fig. 2

HABITAT: Gills of *Naso hexacanthus*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 2.

DESCRIPTION (based on 8 whole mounts): Body flattened, oval to elliptical, 1.6–2.2 mm in length, with maximum width of 0.7–1.0 mm at middle third. Opisthohaptor circular, 0.34–0.48 mm in diameter, with scalloped marginal membrane which is 25 $\mu$  wide in the type 2.0 mm long, with about 10(14?) marginal hooklets at somewhat irregular intervals. Immediately behind the central pit of the opisthohaptor there is a pair of large anchors typical of *Benedenia*, 50–90 $\mu$  long, acute anteriorly and terminating in two blunt points posteriorly; middle pair occurring in *Benedenia* lacking entirely, posterior marginal anchor lacking in two out of 8 specimens; when present, it is 25–35 $\mu$  long, very narrow, undulating, almost filiform, terminating in a minute claw posteriorly. Prohaptor oval, saucer-shaped, 0.1–0.2 mm long, with glandular tissue along anterolateral margin; body fold between two prohaptors usually notched in median line. Two pairs of eye spots anterodorsal to pharynx. Pharynx glandular rather than muscular, 0.08–0.12  $\times$  0.12–0.15 mm, without marginal incision. Intestinal limbs ramified, but not united posteriorly.

Testes oval to elliptical, closely juxtaposed in midregion of body, 0.22–0.35  $\times$  0.18–0.33 mm, with two pairs of Goto's organs immediately behind in median field; in the type the granular contents of the organ are massed together anteriorly as if they were about to be emptied into the common efferent duct of the organ which passes forward between the two testes. Vas deferens containing granules of Goto's organ along with sperm at its proximal end between ovary and left testis. After crossing the uterus dorsally the vas deferens turns back on itself, forming an elongate seminal vesicle, and then enters the cirrus pouch at its base. Prostatic reservoir oval to elliptical, 100–180  $\times$  60–100  $\mu$ , situated longi-

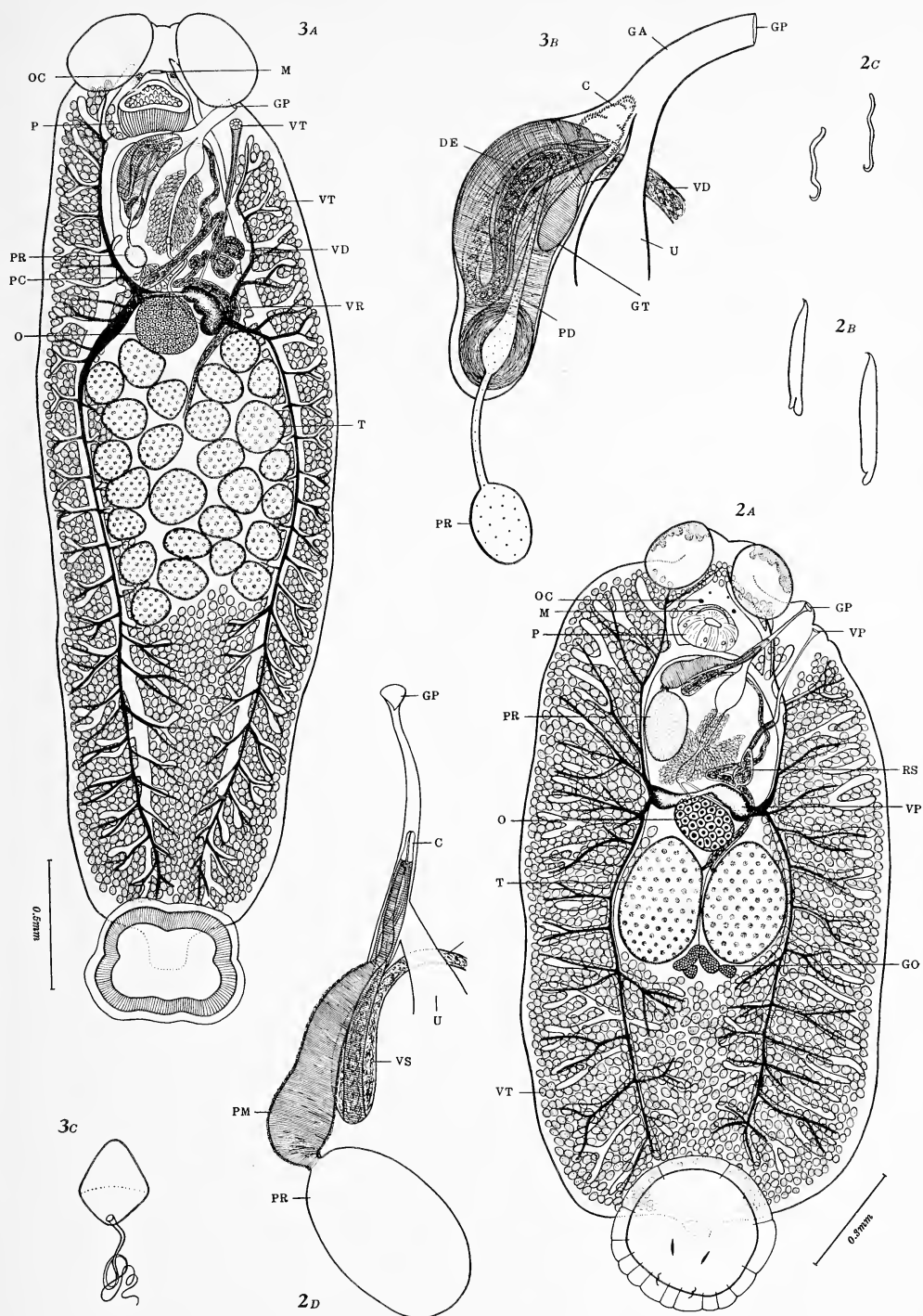


FIG. 2. *Oligoncobenedenia nasonis* n. g., n. sp. 2A, Holotype, ventral view; 2B, anterior haptor anchors; 2C, posterior haptor anchors; 2D, terminal genitalia, ventral view.

FIG. 3. *Pseudonitzschia uku* n. g., n. sp. 3A, Holotype, ventral view; 3B, terminal genitalia, ventral view; 3C, egg.

rudinally between right cecum and seminal vesicle, giving rise to a swollen tubular prostatic duct well provided with circular muscle fibers (pars muscosa). This duct  $110-200 \times 30-60\mu$ , lies transversely along the anterior surface of the seminal vesicle and tapering distally opens into the base of the cirrus pouch from the ventral side. Cirrus pouch subcylindrical, weakly muscular,  $100-175 \times 20-25\mu$ , containing a narrow ejaculatory duct and a narrow muscular prostatic duct, the latter two close parallel to each other. Cirrus rather short, narrow, unarmed. Genital atrium enclosing cirrus pouch, extending but a little beyond the point where the uterus opens into it. Genital pore opening on a prominent marginal papilla projecting immediately posterolateral to left prohaptor at level of eye-spots.

Ovary subglobular, pre-equatorial, median,  $0.13-0.2 \times 0.09-0.14$  mm. Shell gland well developed between prostatic reservoir and ascending vas deferens. Uterus opening into genital atrium close to its base. No eggs observed. Vagina opening at top of a papilliform protuberance on left body margin immediately behind genital pore; vaginal duct running obliquely backward, distinctly muscular for a distance of  $70-80\mu$  before leading into retort-shaped receptaculum seminis vaginae, which is  $80-100 \times 25-60\mu$  and lies in front of the vitelline reservoir, separated dorsally from this by the vas deferens. Vitellaria co-extensive with intestinal branches; vitelline reservoir anterosinistral to ovary,  $40-80 \times 70-130\mu$ .

DISCUSSION: The present genus is distinguished from *Benedenia* Dies., 1858, by possessing two pairs, occasionally only one pair, of haptoral anchors, and by the structure of the male terminalia. It is defined as follows.

### *Oligoncobenedenia* n. g.

GENERIC DIAGNOSIS: Capsalidae, Benedeniinae: Prohaptor in form of suctorial saucers, opisthohaptor with scalloped marginal membrane, provided usually with two pairs, occasionally one pair, of anchors similar to those of *Benedenia*. Pharynx not muscular. Intestinal limbs branched, not united posteriorly. Testes entire, juxtaposed in midregion of body; Goto's glands present. Vas deferens dilated and turning back on itself just before entering base of cirrus pouch. Prostatic

reservoir with its distal portion differentiated into swollen tubular pars muscosa, which penetrates the cirrus pouch at its base. Cirrus pouch weakly developed, enclosing a narrow muscular prostatic duct and a narrow ejaculatory duct; cirrus short, unarmed. Genital atrium extending to near base of cirrus pouch, opening on a prominent marginal papilla projecting immediately posterolateral to left prohaptor. Ovary entire, median, pretesticular. Vagina opening on left body margin immediately behind genital pore; vaginal duct muscular for a short distance before leading into receptaculum seminis vaginae. Vitelline reservoir anterosinistral to ovary. Parasitic on marine teleosts.

TYPE SPECIES: *O. nasonis* n. sp., on gills of *Naso hexacanthus*; Hawaii.

### 3. *Pseudonitzschia uku* n. g., n. sp.

Fig. 3

HABITAT: Gill of *Aprion virescens* (local name "uku"); Hawaii.

HOLOTYPE: U. S. Nat. Mus., Helm. Coll., S.Y. No. 3.

DESCRIPTION (based on 16 whole mounts): Body flattened subcylindrical, 2.15–3.7 mm long, with maximum width of 0.5–1.1 mm at level of midregion. Opisthohaptor discoid, attached to body proper halfway between anterior margin and center of disc, with thickened muscular margin distinctly notched midlaterally and inconspicuously at posterolateral margin and flat posterior margin. Delicate marginal membrane present, but anchors and marginal hooklets entirely absent. Prohaptor glandular, saucer-shaped, 0.28–0.4 mm long. One pair of eye spots anterodorsal to pharynx. Pharynx  $0.08-0.24 \times 0.1-0.28$  mm, without lateral constriction. Esophagus practically absent. Intestinal limbs with side branches, extending to near opisthohaptor without uniting together.

Testes rounded, 20–30 in number (most commonly 25–28), arranged in one layer, occupying anterior part of postovarian interintestinal field. Vas deferens frequently more or less swollen, rarely convoluted at very beginning between ovary and anterior testes, running forward along left margin of vitelline reservoir and then thrown into convolutions anterior to this reser-

voir; after crossing the distal end of the uterus dorsally it comes to lie on the dorsal side of the cirrus pouch where it enters the cirrus pouch and turning back on itself leads into the muscular ejaculatory duct. Ejaculatory duct joining narrow prostatic duct at base of cirrus; latter short conical, projecting into genital atrium, covered all over with very small recurved spines; from the base of the cirrus arises a claviform muscular gonotyl which is about  $100 \times 40 \mu$  in the type and directed obliquely backward. Cirrus pouch subcylindrical, curved,  $0.22-0.4 \times 0.08-0.15$  mm, situated almost longitudinally behind pharynx, provided with circular and oblique muscle fibers. Prostatic reservoir ovoid,  $75-140 \times 60-140 \mu$ , posterior to cirrus pouch; prostatic duct a little swollen and enclosed in a prominent muscle bulb of oblique fibers at posterior end of cirrus pouch, then running straight forward within cirrus pouch and finally uniting with ejaculatory duct. Genital atrium cylindrical, enclosing cirrus pouch, receiving uterus at level of cirrus, opening ventrally beneath left prohaptor.

Ovary subglobular,  $0.12-0.24 \times 0.08-0.21$  mm, situated nearly in median line at posterior end of anterior third of body. Ootype and shell gland well developed between cirrus pouch and convoluted vas deferens. Uterus opening into genital atrium distal to cirrus; eggs one at a time, pentagonal, about 0.1 mm in diameter, with filament at one pole. Vagina lined with thick corrugated cuticle, opening dorsally near left margin of body at level of pharynx; vaginal duct with fusiform swelling distally, united with vitelline reservoir near its distal end; no receptaculum seminis vaginae. Vitellaria co-extensive with intestine; vitelline reservoir on left side of ovary, more or less curved toward ovary,  $0.1-0.23 \times 0.06-0.12$  mm.

DISCUSSION: This new genus is characterized by the opisthohaptor being unarmed, although in general anatomy it resembles *Nitzschia* Baer, 1826. It is separated from all the known subfamilies of Capsalidae as representing a new subfamily on account of this unarmed opisthohaptor.

#### *Pseudonitzschia* n. subf.

SUBFAMILY DIAGNOSIS: Capsalidae. Opisthohaptor disc-shaped, unarmed, with indented

muscular margin and delicate marginal membrane, without septa, loculi, or papillae. Prohaptors saucer-shaped, paired. One pair of eye spots. Pharynx without constriction. Intestinal limbs with side branches, not united posteriorly. Testes numerous, confined to anterior postovarian interintestinal field. Vas deferens convoluted anterior to vitelline reservoir. Cirrus pouch muscular, postpharyngeal, enclosing ejaculatory duct and prostatic duct; cirrus short, armed. A muscular gonotyl present in genital atrium. Common genital pore opening ventrally beneath left prohaptor. Ovary entire, pretesticular. Ootype well developed. Uterus opening into genital atrium distal to male pore. Vagina opening dorsally close to left margin of body at level of pharynx. No receptaculum seminis vaginae. Vitellaria co-extensive with intestinal limbs and their branches. Vitelline reservoir immediately sinistral to ovary. Gill parasites of marine teleosts.

#### *Pseudonitzschia* n. g.

GENERIC DIAGNOSIS: Capsalidae, Pseudonitzschinae: With characters of subfamily.

TYPE SPECIES: *P. uku* n. sp., on gills of *Aprion virescens*; Hawaii.

#### 4. *Diplobheterocotyla dasyatis* n. g., n. sp.

##### Fig. 4

HABITAT: Gill of *Dasyatis* sp. (? *D. hawaiiensis*); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 4.

DESCRIPTION (based on 7 whole mounts): Body elliptical in outline;  $0.9-1.2 \times 0.3-0.53$  mm, covered with smooth cuticle. Opisthohaptor circular,  $2.12-3.15 \mu$  in diameter, divided into a round central loculus  $65-115 \mu$  across and eight muscular marginal loculi, provided with a marginal membrane up to  $30-35 \mu$  wide and a pair of anchors measuring  $27-33 \mu$  long lineally from tip of ventral root to height of curve of blade and  $35-53 \mu$  lineally from tip of dorsal root to height of curve of blade; dorsal root inserted deeply into the septum between posterior submedian and posterolateral loculi. Marginal hooklets hardly recognizable at each interocular marginal notch. Oral sucker subterminal,  $65-100 \times 100-155 \mu$ , surmounted on its anterodorsal border by a transversely elongated pillow-like lobe.



Pharynx globular, 62–85 $\mu$  in diameter; prepharyngeal portion well differentiated from muscular pharynx. Ceca wide, with short inner and longer outer branches, terminating dorsal to opisthohaptor where the most medial branches appear to be united together.

Testes oval, about 100 $\mu$  long, almost symmetrical, one on each side of median ovarian curvature. Vas deferens turning round the bulbus ejaculatorius and penetrating it at its posterior end, forming two dilatations, one immediately in front of the bulbus and the other immediately behind the bulbus, both serving as seminoprostatic reservoirs, because they contain spermatozoa and prostatic granules secreted from the neighboring prostatic cells. Bulbus ejaculatorius 75–110  $\times$  57–80 $\mu$ , containing abundant granules in wide space between its wall of circular muscles and the ejaculatory duct. Copulatory organ consisting of a well sclerotized, tubular, cirrus proper which is 30–45 $\mu$  long, more or less flared at each end and provided sideways with a sclerotized fold, and of a bundle of about 10, slightly curved, slender, accessory spines. To the base of the cirrus are attached special whirling muscle bundles merging into surrounding body parenchyma, probably associated with movements of the cirrus; the cirrus and its accessory spines project backwards toward the ventral genital pore situated immediately in front of the uterine pore.

Ovary 75–150  $\times$  150–250 $\mu$ , just postequatatorial; its greater proximal portion V-shaped, with its end more or less swollen and its right arm embracing right cecum. The germiduct arising from the distal end of the ovary joins the common vitelline duct and the duct from the vaginal seminal receptacle medial to the swollen proximal end of the ovary; the fertilization canal describes a sigmoid curve and after being surrounded by shell glands of two different types leads into the uterus proper. The latter is funnel-shaped, with distinct epithelial lining, opening midventrally by a large rounded aperture behind male pore. Eggs mitral, 75–83 $\mu$  long by 75–83 $\mu$  wide in life, 95–100  $\times$  80–95 $\mu$  in mounted condition, with prominent posterior lateral ends, from one of which arises the fine filament. Vagina strongly sclerotized basally, opening ventrally medial to left intestinal limb. Recep-

taculum seminis rounded, 40–60 $\mu$  in diameter, enclosed in proximal portion of vagina. Vitellaria co-extensive with intestine; transverse vitelline duct equatorial.

DISCUSSION: This monocotylid genus differs from any other members of the subfamily Monocotylinae by possessing two testes instead of one, although resembling *Heterocotyle minima* (MacCallum, 1916) Price, 1938, in general anatomy. The generic name refers to this feature.

*Diplobheterocotyla* n. g.

GENERIC DIAGNOSIS: Monocotylidae, Monocotylinae: No eye spots. Opisthohaptor divided by eight septa into eight muscular marginal loculi and nonmuscular central loculus, with one pair of anchors. Interlocular marginal hooklets hardly recognizable. No other sclerotized structures on opisthohaptor. Oral sucker surmounted anterodorsally by transversely elongated lobe. Pharynx strongly muscular, preceded by special prepharyngeal structure. Intestinal limbs with side branches, terminating dorsal to opisthohaptor. Testes two, subsymmetrical behind ovary. Bulbus ejaculatorius well developed, with wide space filled with fine granules between its wall of circular muscles and the ejaculatory duct penetrating it. Copulatory organ consisting of a well sclerotized, tubular cirrus proper, and a bundle of slender accessory spines; male genital pore immediately in front of uterine pore. Ovary curved, immediately pretesticular, embracing right intestinal limb. Uterine pore midventral, behind male pore; eggs mitral, filamented at one posterolateral end. Vitellaria co-extensive with intestine. Vagina present. Receptaculum seminis enclosed in vagina. Parasitic on gills of elasmobranchs.

TYPE SPECIES: *D. dasyatis* n. sp., on *Dasyatis* sp.; Hawaii.

5. *Neobaliootrema maomao* n. g., n. sp.

Fig. 5

HABITAT: Gill of *Abudefduf abdominalis* (local name "maomao"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 5.

DESCRIPTION (based on 25 whole mounts): Body very small, elongate, 0.23–0.44 mm long, up to 60–90 $\mu$  wide in midregion. Opisthohaptor



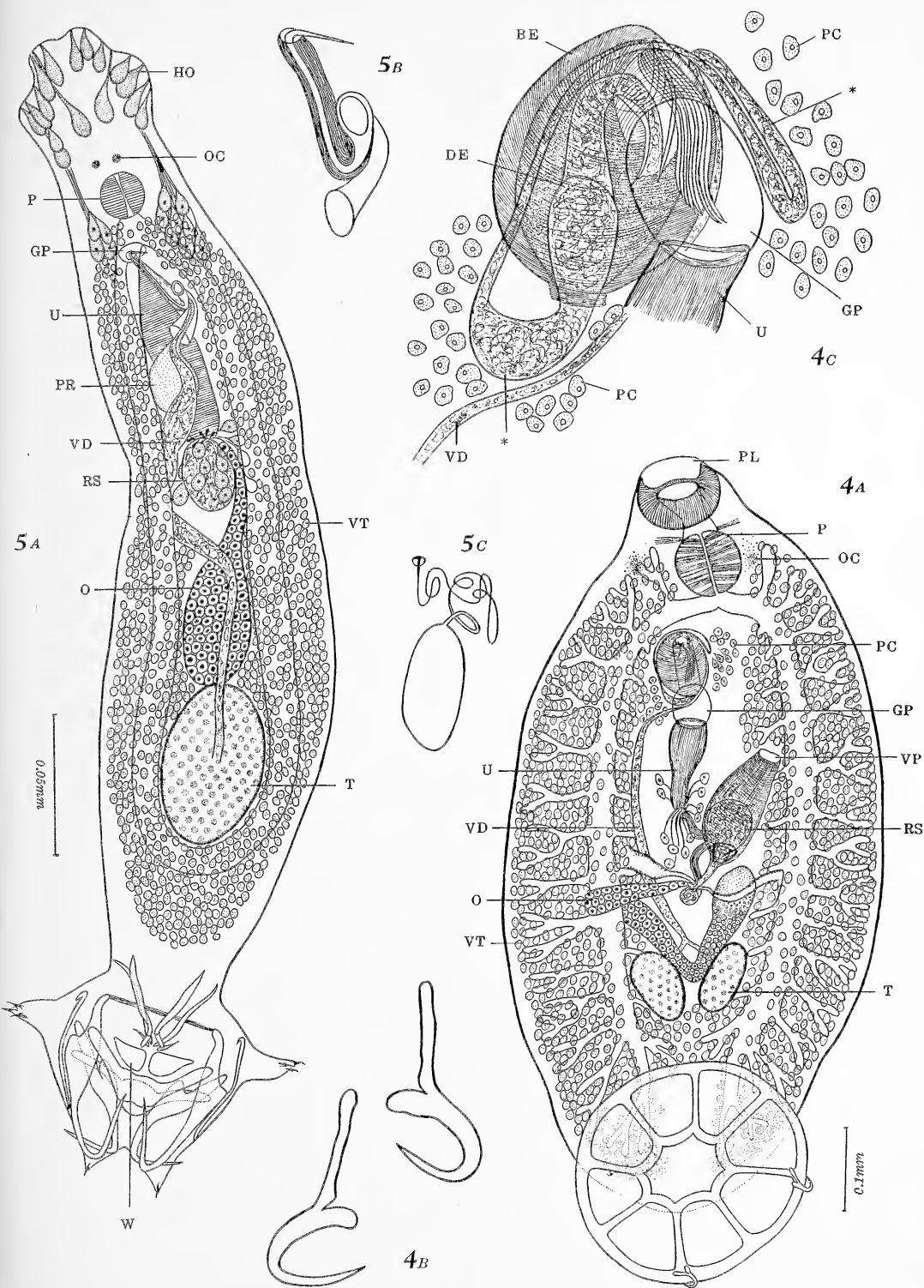


FIG. 4. *Diplobheterocotyla dasyatis* n. g., n. sp. 4A, Holotype, ventral view; 4B, haptoral anchors; 4C, terminal genitalia, ventral view.  
FIG. 5. *Neobaliootrema maomao* n. g., n. sp. 5A, Holotype, dorsal view; 5B, cirrus; 5C, egg.

well marked off from body proper, 42–100 $\mu$  wide at level of hornlike lateral projections, each tipped with a marginal hooklet about 10 $\mu$  long; at this level there is a pair of spines 25–35 $\mu$  long in form of a V in the dorsal median field with acute points directed anterolaterad; immediately ventrolateral to this is another pair of very slender spines of nearly the same length together with the anterior median pair of marginal hooklets; dorsal anchor 40–60 $\mu$  long from tip of dorsal root to height of curve of blade; dorsal bar V-shaped, 25–50 $\mu$  transversely from end to end; ventral anchor 32–53 $\mu$  long from tip of ventral root to height of curve of blade; ventral bar overlapping dorsal, curved angularly on each side of median line, 32–53 $\mu$  transversely from end to end. It is very interesting to note that there is a pair of round windows separated by a narrow median string of tissue immediately in front of the median bars. Head with two inconspicuous lobes studded with head organs on each side. Very conspicuous head glands massed together posterolateral to pharynx. Only one pair of compact eye spots immediately anterior to pharynx. Pharynx 12–20  $\times$  12–19 $\mu$ ; esophagus practically absent. Intestinal limbs united posterior to testis.

Testis elliptical, 25–81  $\times$  17–42 $\mu$ , situated at junction of middle with posterior third of body. Vas deferens running forward ventral to left intestinal limb, distended with sperm, up to 12 $\mu$  wide, and opening into base of cirrus. Cirrus narrow, tubular, twisted, sheathed except for base and pointed distal portion. Prostatic reservoir tubular or claviform, 6–9 $\mu$  wide, immediately behind cirrus, with its base directed backwards. Prostatic cells massed together around base of prostatic reservoir.

Ovary retort-shaped, 25–47  $\times$  12–26 $\mu$ , situated obliquely immediately in front of testis, with its distal end produced anteriorly. Shell gland complex rosette-shaped, very conspicuous. Vagina very much reduced; its rudiment may be recognizable ventral to seminal receptacle. Latter oval, 13–23  $\times$  10–16 $\mu$ . A large shrunken egg 70–77  $\times$  37–39 $\mu$  was often observed hanging out of genital pore, with its posterior polar filament 0.18–0.32 mm long enlarged at tip. Vitellaria co-extensive with intestine.

**DISCUSSION:** This species is characterized by possessing two pairs of spiniform sclerites on the dorsal side of the base of the opisthohaptor and a pair of round windows behind the sclerites; the vas deferens runs forward ventral to the left intestinal limb without looping around it. Of the eye spots there is only one pair, without exception. Considering all these features combined, I venture to propose a new genus, for which *Neohaliotrema* is suggested, because of resemblance to *Haliotrema* in other characters.

### *Neohaliotrema* n. g.

**GENERIC DIAGNOSIS:** Dactylogyridae, Ancyrocephalinae: Body elongate, very small. Opisthohaptor distinctly set off from body proper, with two pairs of anchors, two haptoral bars, small number of marginal hooklets and two pairs of slender spiniform sclerites, perforated between bars and spiniform sclerites by a window which is separated into two by a narrow median string of tissue. Only one pair of compact eye spots, exceptionally a single one, present. Intestinal crura simple, united posteriorly. Testis in posterior half of body; vas deferens distended with sperm, running forward ventral to left intestinal crus without looping around it. One prostatic reservoir present. Cirrus tubular, twisted, swollen at base, partly sheathed, without accessory piece. Genital pore median or nearly so. Ovary pretesticular, oblong. Vagina rudimentary or absent. Receptaculum seminis present. Vitellaria co-extensive with intestine. Parasitic on gills of marine teleosts.

**TYPE SPECIES:** *N. maomao* n. sp., on *Abudefduf abdominalis*; Hawaii.

### 6. *Pseudempleurosoma carangis* n. g., n. sp.

Fig. 6

**HABITAT:** Gill and pharynx of *Caranx lugubris* (type host), *Caranx sexfasciatus*, and *Myripristis berndti*; Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 6.

**DESCRIPTION** (based on 30 whole mounts): Body flattened subcylindrical, 0.8–1.32  $\times$  0.15–0.34 mm, tapered posteriorly. Opisthohaptor shallowly constricted off from body proper, truncate behind, 70–90 $\mu$  wide, with two pairs of dissimilar anchors and 14 marginal hooklets 10–

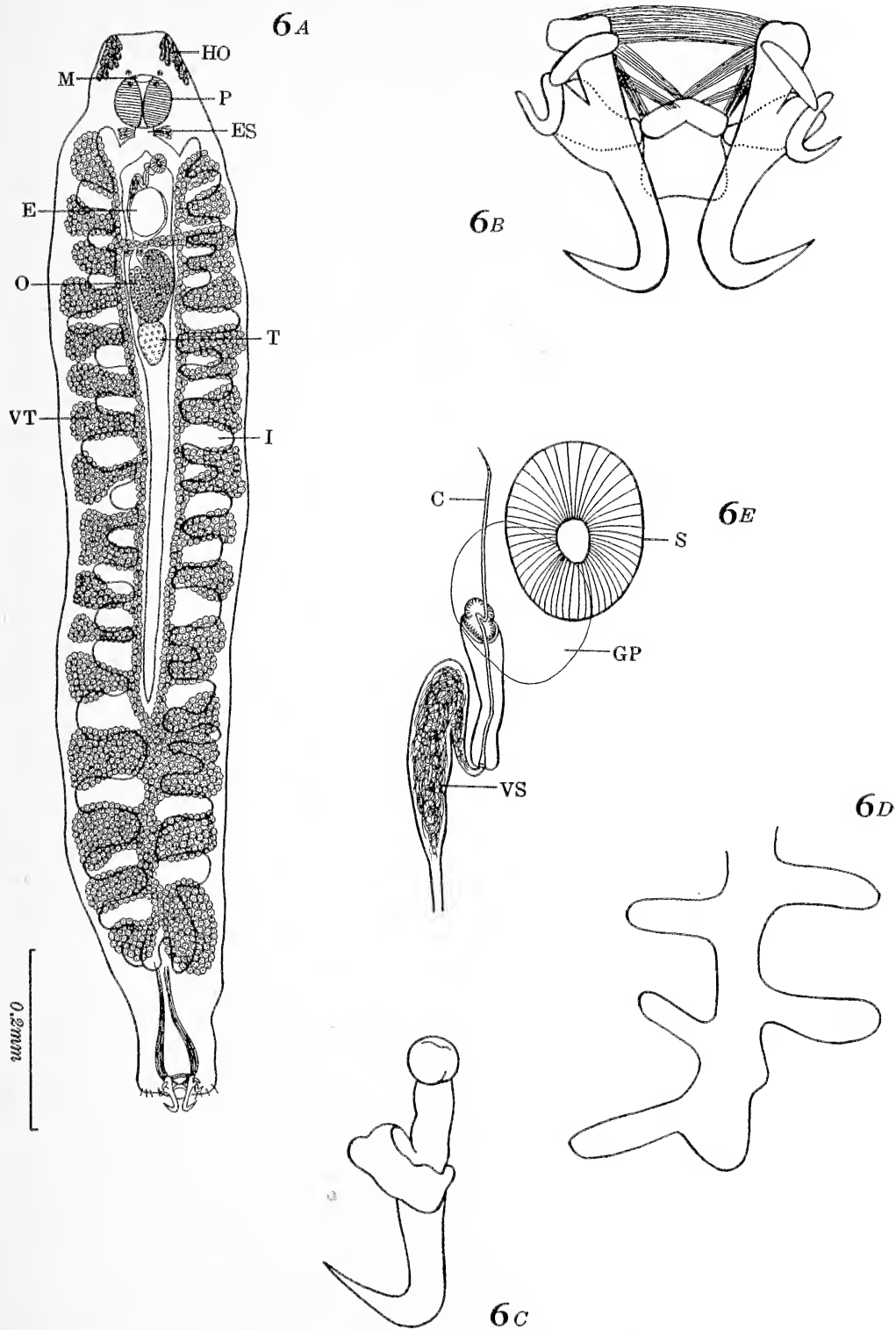


FIG. 6. *Pseudempleurosoma carangis* n. g., n. sp. 6A, Holotype, ventral view; 6B, anchor apparatus, ventral view; 6C, dorsal anchor, dorsal view; 6D, intestine; 6E, terminal genitalia, ventral view.

15 $\mu$  long; anterior medial hooklets abnormally large; dorsal anchor stout, 47–53 $\mu$  from tip of ventral root to height of curve of blade, its dorsal root shorter than ventral root, turned medially to form a dorsal swelling, at the inner end of which the anchor articulates with its fellow of the other side by means of a median bar; this bar looks like an approximately quadrangular shield, but its convex anterior border, 12.5–15 $\mu$  lineally from end to end, is thickened in form of an inverted V or an arc. The muscle fibers coming from the ventral median body wall are mainly attached to the dorsal root, whereas the ventral roots of the two stout anchors are connected with each other by a broad muscle band. Ventral anchor very small, simple, only 10–15 $\mu$  long, wider apart one from the other than stout dorsal anchors, with its root articulated with a simple oblique bar about 15 $\mu$  long. Head trapezoidal, with a compact group of head glands anterolaterally. Two pairs of eye spots dorsal to mouth. Pharynx globular, 45–65  $\times$  57–75 $\mu$ . Esophagus wide, up to 40–50 $\mu$  long, with a group of gland cells on each side; the ducts of these gland cells are directed toward the posterior end of the pharynx. Ceca comparatively wide, united posterior to testis at a variable distance in different individuals, sometimes far posteriorly, each with a number of undivided diverticula laterally; posterior common cecum also with diverticula on each side, terminating blindly some distance anterior to opisthohaptor.

Testis round to oval, 32–85  $\times$  25–60 $\mu$ , median, toward middle of anterior half of body. Vas deferens passing along right margin of ovary, leading to small seminal vesicle which lies at the base of the copulatory apparatus. Cirrus tubular, slender, about 50 $\mu$  long, enclosed in a cylindrical sheath for its proximal portion, but free in the distal portion and twisted at the junction of the two portions just at the level of the distal end of the sheath which is armed with a circle of very fine spiniform structures. Genital atrium median, just postbifurcal; into this atrium projects a small, muscular, acetabular disc 22–30 $\mu$  in diameter from the anterolateral side; the postero-medial border of the disc sometimes showing in the postbifurcal median genital pore.

Ovary 50–100  $\times$  50–78 $\mu$ , turned back on itself between testis and transverse vitelline duct,

with its distal end turned forward. Neither seminal receptacle nor vagina. Eggs oval, without polar filament, about 90  $\times$  70 $\mu$  in life, one at a time. Vitellaria forming numerous transversely elongated lobes intercalated between cecal diverticula and connected medially with paired longitudinal vitelline ducts commencing at level of intestinal bifurcation or genital pore; some of the posterior lobes of the two sides are confluent, although the level of the anterior limit of this union varies individually.

DISCUSSION: This genus resembles *Diplectanotrema* Johnston and Tiegs, 1922 on the one hand, and *Empleurosoma* Johnston and Tiegs, 1922, on the other; the differences are shown in the following table:

	<i>Diplectanotrema</i>	<i>Empleurosoma</i>	<i>Pseudempleurosoma</i>
Intestinal ceca	separate	united posteriorly	united posteriorly
Vagina	present	absent	absent
Receptaculum seminis	present	?	absent
Vitellaria	separate	separate	confluent posteriorly

### *Pseudempleurosoma* n. g.

GENERIC DIAGNOSIS: Dactylogyridae, Ancyrocephalinae: Body more or less uniform in width; opisthohaptor truncate, shallowly constricted from body proper, with 14 marginal hooklets, of which the anterior medial pair is unusually large, 2 pairs of dissimilar anchors, an unpaired median shieldlike bar for larger anchors, and paired rod-shaped bars for smaller, widely separated anchors. Two pairs of eye spots present. Esophagus short, with gland cells on each side; ceca with numerous lateral diverticula, confluent posteriorly and terminating a short distance anterior to opisthohaptor. Testis about middle of anterior half of body; seminal vesicle near base of copulatory apparatus. Cirrus tubular, slender, enclosed in sheath proximally but free distally. Genital pore median, postbifurcal. A small, muscular, acetabular disc projecting into genital atrium. Ovary immediately pretesticular, turned back on itself. Neither seminal receptacle nor vagina. Eggs without polar filament, produced one at a time. Vitellaria divided into numerous, transversely elongated lobes, co-extensive with ceca

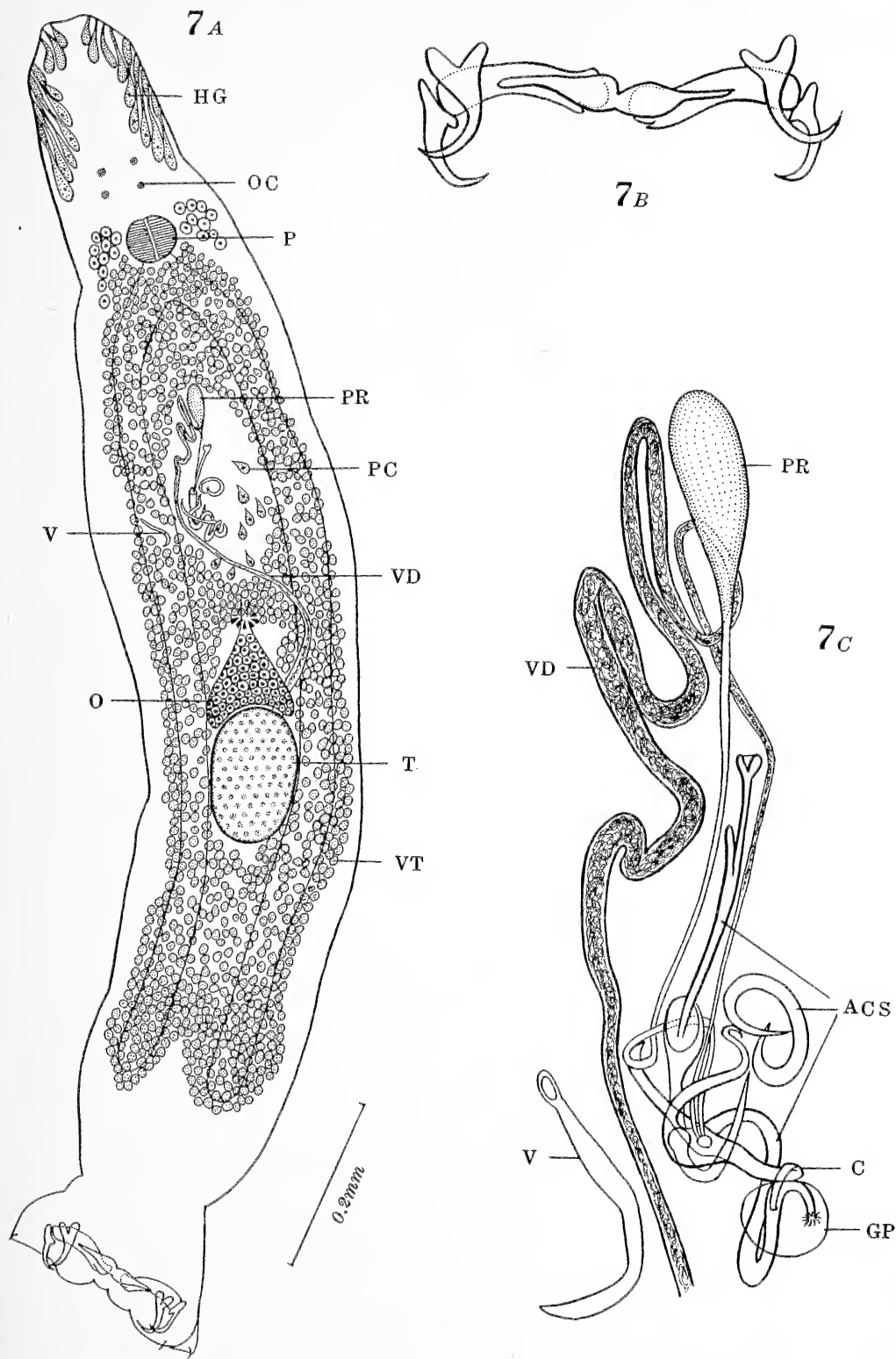


FIG. 7. *Nasobranchitrema pacificum* n. g., n. sp. 7A, Holotype, ventral view; 7B, anchor apparatus, ventral view; 7C, terminal genitalia, ventral view.

and their diverticula, united posteriorly; transverse vitelline duct and shell gland immediately preovarian. Gill parasites of marine teleosts.

TYPE SPECIES: *P. carangis* n. sp., on *Caranx lugubris*; *C. sexfasciatus*, and *Myripristis berndti*; Hawaii.

#### 7. *Nasobranchitrema pacificum* n. g., n. sp.

Fig. 7

HABITAT: Gills of *Naso hexacanthus* (type host), *Naso lituratus*, and *N. brevirostris*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 7.

DESCRIPTION (based on 12 whole mounts): Body elongate subcylindrical, slightly tapering anteriorly, 0.95–1.5 mm long, 0.11–0.26 mm wide at level of testis. Opisthohaptor 0.14–0.25 mm wide, well set off from body proper, with two pairs of anchors, 3 separate bars, and several pairs of marginal hooklets about  $10\mu$  long at level of lateral prominences; dorsal anchors 45–55 $\mu$  long lineally from tip of longer dorsal root to height of curve of blade, dorsal to lateral portion of ventral bar; ventral anchor 35–50 $\mu$  long lineally from tip of base to height of curve of blade, with its obliquely flattened base articulating with ventral bar; of the three separate bars, the unpaired median dorsal 50–80 $\mu$  long is constricted at middle, each half swollen medially and resting on transverse dorsal ledge of submedian bar, tapered laterally; submedian bars meeting in median line, 55–80 $\mu$  long, each swollen at medial portion bearing above mentioned transverse ledge. Head trapezoidal, 0.07–0.15 mm wide at base, with several head organs along each lateral sloping margin; head glands well developed laterally at level of pharynx. Two pairs of eye spots anterior to pharynx. Pharynx globular, 27–80 $\mu$  in diameter. Esophagus practically absent. Ceca simple, terminating separately posterior to testis at about middle of posterior third of body.

Testes oval,  $0.1\text{--}0.2 \times 0.045\text{--}0.12$  mm, situated at posterior end of middle third of body. Vas deferens running forward by right side of ovary and then along medial side of right intestinal limb, passing between copulatory organ and vagina, and describing N-shaped curve in right anterior intercecal area; ejaculatory duct

running backward alongside efferent duct of prostatic reservoir. Copulatory organ complex in structure; main portion consisting of C-shaped cirrus from which two winding tubules arise in opposite directions, one reaching to a ringlike independent tubular structure and the other looping around the distal portion of the cirrus which turns back on itself to open into the genital pore. The proximal portion of the cirrus is produced forward into a clawlike structure, but there is another wide cuticular tube arising from near origin of the two above mentioned tubules and terminating in a slight enlargement where the ejaculatory duct and the prostatic ducts empty into the cirrus. Prostatic reservoir elongate oval to elliptical,  $40\text{--}75 \times 25\text{--}50\mu$ , behind intestinal bifurcation, with its descending duct running alongside descending ejaculatory duct and opening into base of cirrus. Genital pore nearly median, some distance posterior to intestinal bifurcation.

Ovary heart-shaped or irregular in shape,  $50\text{--}100 \times 30\text{--}100\mu$ , immediately pretesticular, with shell gland complex in front. Vagina represented by a well cuticularized undulating, probably non-functional, tubule about 50 $\mu$  long and lying obliquely posterodextral to the copulatory organ. It is not certain whether it opens outside ventrally or not. Vaginal duct narrow, descending from proximal end of vagina toward shell gland complex. No seminal receptacle. Shrunken egg observed *in utero* is about 80 $\mu$  long, produced backward into a rigid filament. Vitellaria co-extensive with intestine; transverse vitelline duct in front of shell gland complex.

DISCUSSION: This genus is characterized by the possession of three separate haptoral bars and a very complex copulatory organ. From the structure of the haptoral apparatus there is no doubt that it belongs to the Diplectanidae Bychowsky, 1957, but differs from any of the known genera of this family by the absence of adhesive plaques or squamodiscs. It is defined as follows:

#### *Nasobranchitrema* n. g.

GENERIC DIAGNOSIS: Diplectanidae without adhesive plaques or squamodiscs. Body elongate, subcylindrical, very small. Opisthohaptor well marked off from body proper, with two pairs of anchors and three separate haptoral bars, of

which the median is constricted into two portions, the paired submedian meeting in the median line. Two pairs of eye spots present. Intestinal limbs simple, terminating separately behind testis. Testis postequatorial; vas deferens not looping around intestinal limb, winding behind intestinal bifurcation. Copulatory organ complex in structure. Prostatic reservoir present. Genital pore some distance postbifurcal, median or submedian. Ovary pretesticular, with shell gland complex in front. Vagina present. Vitellaria co-extensive with intestine. Eggs produced backward into rigid filament. Gill parasites of marine teleosts.

TYPE SPECIES: *N. pacificum* n. sp., on *Naso hexacanthus*, *N. lituratus*, *N. brevirostris*; Hawaii.

8. *Pseudodictyophora decapteri* n. g., n. sp.

Fig. 8

HABITAT: Gills of *Decapterus pinnulatus* (local name "opelu"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 8.

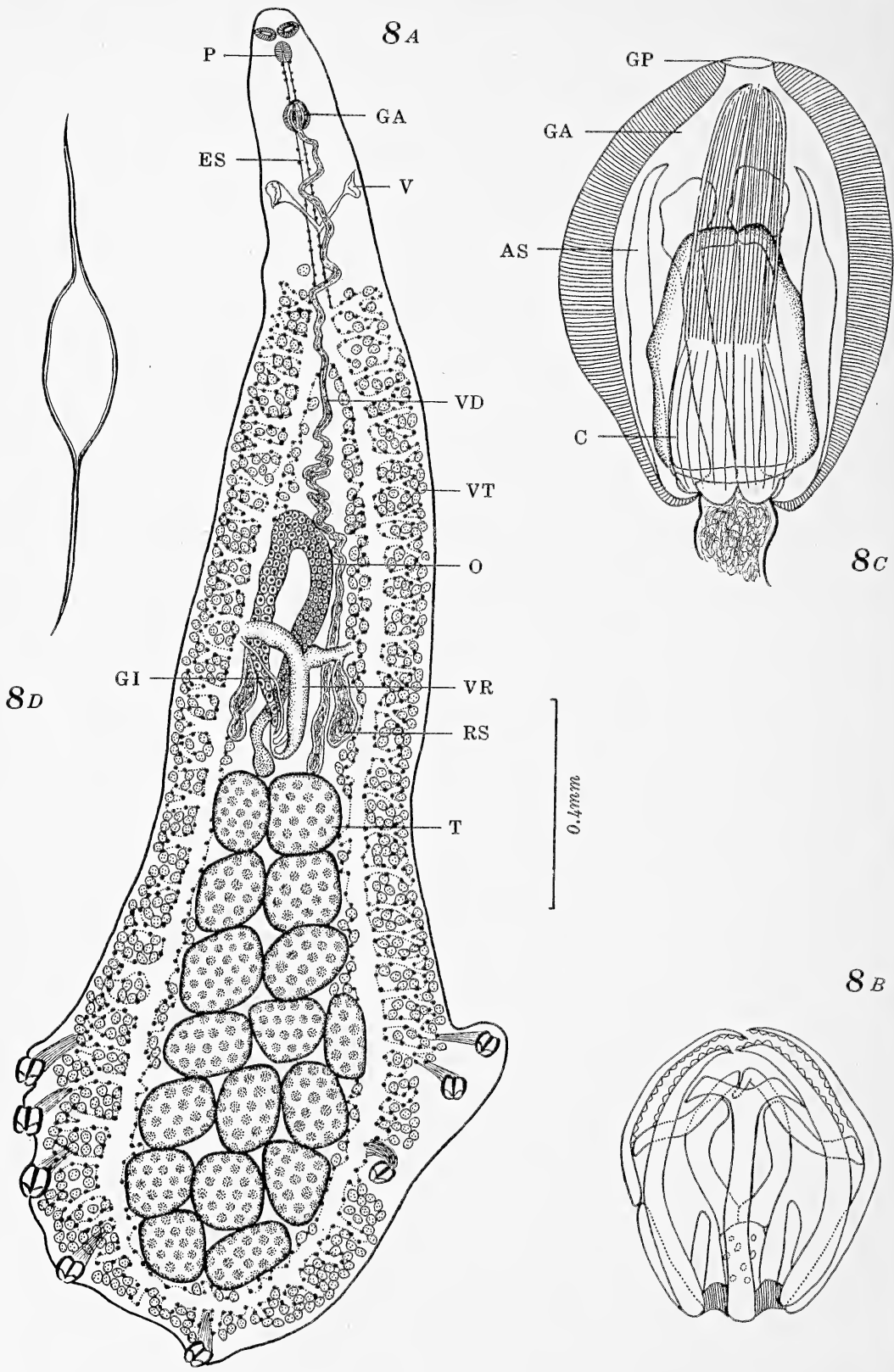
DESCRIPTION (based on 21 whole mounts): Body 1.5–2.9 mm long, tapering anteriorly and rounded posteriorly, 0.35–0.7 mm wide immediately in front of opisthaptor. Opisthaptor extending asymmetrically along each posterior lateral margin of body, but separated at the truncate posterior end of body, consisting of 4 pairs of asymmetrically arranged sessile clamps. On the right side the fourth clamp is more or less wider apart from the third than the second is from the first, and on the left side the fourth clamp is separated from the third by a convex body margin 0.17–0.5 mm long; the third clamp is also wider apart from the second just like the third on the right. Clamp skeleton of the right side consisting of a U-shaped median piece, a pair of small basal pieces, 2 pairs of lateral springs and a pair of accessory sclerites; median piece widely bifid at end of ventral prong; shorter dorsal prong with U-shaped apical piece, surmounted by accessory sclerites. One of the lateral sclerites is much thinner than its fellow of the same side, almost membranous; the inner lateral sclerites nearly of same thickness. One of the accessory sclerites distinctly longer than its partner. Basal pieces not projecting into lumen

of clamp valve. Skeleton of left clamp different from that of right clamp; dorsal prong of U-shaped median piece divided into dissimilar branches, of which the larger articulates with the medial projection from the outer lateral sclerites on one side and also with the larger piece of the  $\lambda$ -shaped accessory sclerites on the other; two lateral sclerites of the outer side strongly developed, and denticulated distally on opposite sides, whereas one of those on the inner side is reduced to non-sclerotized piece, though its basal portion is distinctly sclerotized like that of its partner. Head 88–100 $\mu$  wide, with prominent rounded preoral lobe. Prohaptor oral suckers paired as in *Microcotyle*, aseptate, unarmed, 22–43  $\times$  25–53 $\mu$ . Pharynx rounded, 30–43  $\times$  25–43 $\mu$ . Esophagus simple, often very wide, 0.3–0.7 mm long. Ceca with numerous short inner and longer outer branches, confluent at posterior end of body.

Testes large, irregular in outline, 15–30 in number, occupying whole postovarian intercecal field. Vas deferens winding forward medial to left intestine in ovarian region, at the anterior end of which it takes the median course. No pars prostatica differentiated. Cirrus represented by a short cylindrical sclerotized structure opening at its tip and measuring 30–38 $\mu$  long by 15–23 $\mu$  wide; it lies ventral to semicircle of six longitudinal cuticular rods 38–50 $\mu$  long. This coronet in turn is enclosed in genital atrium provided with very fine circular muscle fibers. This atrium, 45–50  $\times$  30–47 $\mu$ , opens midventrally at a distance of 0.16–0.33 mm from head end.

Ovary inverted U-shaped, 0.25–0.6  $\times$  0.05–0.16 mm, situated in midregion of body with its proximal end on the right of vitelline reservoir and its distal end near genitointestinal duct. The latter duct arising from the germiduct just anterior to the junction of the germiduct with the vitelline reservoir runs obliquely forward and opens into the right intestine at the level of the two arms of the vitelline reservoir. Uterus ventromedian, apparently opening at common genital pore; eggs 180–220  $\times$  60–90 $\mu$ , with rigid filament 140–200 $\mu$  long at each end. Vitellaria co-extensive with intestine and its branches; vitelline reservoir Y-shaped; its stem just postequatorial, 0.1–0.24 mm long, largely overlapping ovary. A pair of elongate saccular seminal







receptacles filled with sperm, occasionally also with a mass of yolk cells, connected with arms of vitelline reservoir just medial to intestine, that of the same side as the vas deferens lies between the vas deferens and the intestine of that side. I propose to call this receptacle "receptaculum seminis vitellariorum." Vagina funnel-shaped, symmetrical, marginal, 0.28–0.6 mm from head end, nearer to genital pore than to intestinal bifurcation; vaginal ducts of two sides joining together in form of V, but no duct communicating with the vitelline reservoir has been detected.

**DISCUSSION:** This genus apparently belongs to *Diclidophoroidea* Price, 1936, but cannot be placed in any known families of this superfamily because of the constant peculiar asymmetry of the opisthohaptor and the presence of symmetrical seminal receptacles connected with the arms of the vitelline reservoir in full-grown specimens. That the vaginal ducts are united and have connection neither with the vitelline reservoir nor with the seminal receptacles is worth noting.

#### ***Pseudodiclidophorinae* n. subf.**

**SUBFAMILY DIAGNOSIS:** *Pseudodiclidophoridae*: Opisthohaptor asymmetrical, with four pairs of clamps along posterolateral margin of body. No anchor-bearing caudal appendage.

#### **PSEUDODICLIDOPHORIDAE n. fam.**

**FAMILY DIAGNOSIS:** *Diclidophoroidea*: Opisthohaptor developed on posterior lateral part of body as marginal frills carrying 4 pairs of asymmetrical or symmetrical sessile clamps; each clamp with accessory sclerites. Caudal appendage present or absent. Symmetrical prohaptor suckers in buccal cavity. Intestinal crura with numerous branches, confluent posteriorly. Testes postovarian, variable in number. Copulatory organ complex in structure. Common genital pore median, esophageal. Ovary turned back on itself, pretesticular. Genito-intestinal duct present. Symmetrical seminal receptacles connected with vitelline reservoir. Vagina present. No communication between vagina and vitelline reservoir. Vitellaria entirely co-extensive with intestinal crura. Parasites of marine fishes.

**TYPE GENUS:** *Pseudodiclidophora* n. g.

This family includes two subfamilies, *Pseudodiclidophorinae* n. subf. and *Allopseudodiclidophorinae*. These subfamilies can be distinguished one from the other by the opisthohaptor being symmetrical or asymmetrical, by the presence or absence of an anchor-bearing caudal appendage.

#### ***Pseudodiclidophora* n. g.**

**GENERIC DIAGNOSIS:** *Pseudodiclidophoridae*, *Pseudodiclidophorinae*: Body markedly tapered anteriorly. Clamps sessile, 4 on each side of posterior part of body, arranged asymmetrically, the fourth clamp wider apart from the third than the second is from the third, especially on one side; clamp skeleton consisting of 2 pairs of lateral sclerites, an unpaired median piece, accessory sclerites and small basal sclerites. Prohaptor suckers aseptate, unarmed. Esophagus simple, long. Intestinal crura confluent posteriorly. Testes numerous, confined to postovarian interintestinal field. Cirrus forming a small sclerotized cylinder, ventral to semicircle of cuticular rods which is enclosed in the genital atrium of very fine circular muscle fibers. Common genital pore ventromedian, far anterior to intestinal bifurcation. Ovary inverted U-shaped, in midregion of body, with both ends directed backwards. Genito-intestinal duct long, opening into right intestinal crus. Symmetrical seminal receptacles connected with both arms of vitelline reservoir, very conspicuous in full-grown specimens. Eggs with filament at each pole. Vagina symmetrical, vaginal ducts united together, without any connection with vitelline reservoir or seminal receptacles. Vitellaria co-extensive with intestine and its branches. Vitelline reservoir Y-shaped. Gill parasites of marine teleosts.

**TYPE SPECIES:** *P. decapteri* n. sp., on *Decapterus pinnulatus*; Hawaii.

#### **9. *Allopseudodiclidophora opelu* n. g., n. sp.**

Fig. 9

**HABITAT:** Gills of *Decapterus pinnulatus* (local name "opelu"); Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 9.

FIG. 8. *Pseudodiclidophora decapteri* n. g., n. sp. 8A, Holotype, ventral view; 8B, clamp, ventral view; 8C, male terminal genitalia, ventral view; 8D, egg.

**DESCRIPTION** (based on seven whole mounts): Body markedly attenuated anteriorly, 2.9–4.6 mm in length exclusive of anchor-bearing caudal appendage, with maximum width of 0.96–1.8 mm in testicular region. Opisthohaptor symmetrical, consisting of four pairs of small sessile clamps about  $10\mu$  in diameter, extending along posterior margin of body, with caudal appendage between. Clamp skeleton similar to that of *Pseudodidiclidophora decapтери* with  $\lambda$ -shaped accessory piece; the left dorsal sclerite is slender and jointed, whereas the right ventral sclerite is slender and unjointed, so that the lateral sclerites are asymmetrical; median spring bifid at both ends, dorsal prong longer than ventral. Caudal appendage  $0.5\text{--}1.0 \times 0.1\text{--}0.12$  mm, provided at its somewhat swollen distal end with three pairs of hook-shaped anchors; outer anchor  $45\text{--}50\mu$  long, with very prominent guard; middle anchor similar in shape,  $18\mu$  long; inner anchor  $20\text{--}22\mu$  long, also with prominent guard and recurved root. Head rather pointed, about  $0.09\text{--}0.12$  mm wide. Prohaptor oral suckers paired, rounded, aseptate, unspined,  $30\text{--}45\mu$  in diameter; pharynx bulbous,  $35 \times 30\mu$  in the type; esophagus  $0.7\text{--}1.5$  mm long, intestinal limb with short inner and longer outer branches, apparently united with each other at posterior end of body proper.

Testes transversely elongated, irregular in outline,  $12\text{--}30$  in number, occupying whole post-ovarian interintestinal field in two longitudinal rows; vas deferens middorsal, distended with sperm and strongly winding in one of the paratypes, but very narrow and straight in the type. Cirrus terminating in form of a sclerotized cylinder projecting into genital atrium. This cirrus is supported dorsally by a pair of apically incurved rods  $35\mu$  long, a pair of also apically incurved lateral rods  $48\text{--}50\mu$  long and a pair of nearly parallel, apically enlarged, dorsal rods. Genital atrium  $55\text{--}62\mu$  long by  $40\text{--}50\mu$  wide, with wall of circular muscle fibers. Genital pore midventral,  $0.25\text{--}0.68$  mm from head end.

Ovary inverted U-shaped,  $0.4\text{--}0.8 \times 0.15\text{--}0.2$  mm, situated at junction of middle with posterior third of body, with both ends directed

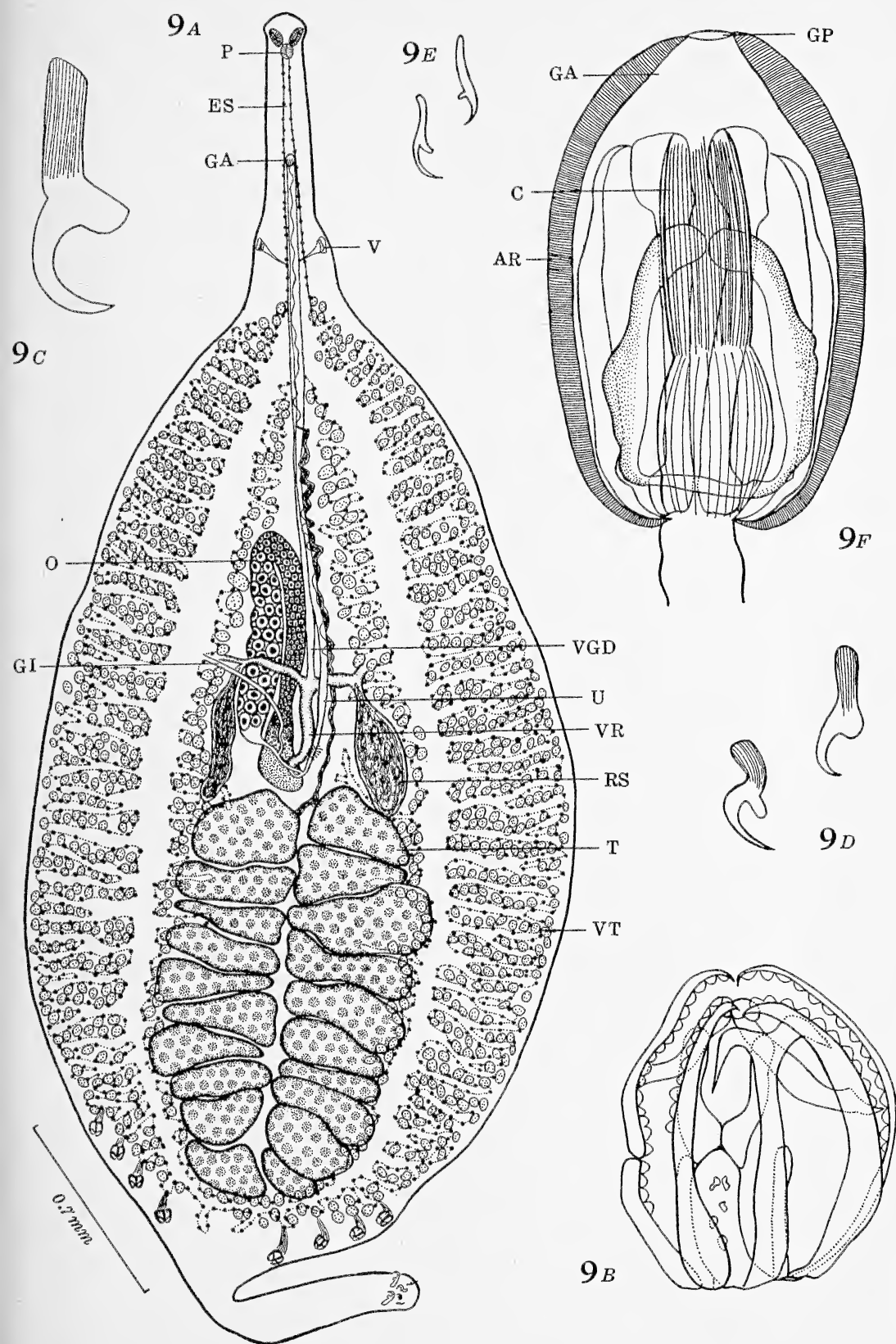
backwards; genito-intestinal canal crossing distal end of ovary and opening into right intestinal limb. One uterine egg observed,  $0.17 \times 0.07$  mm, with rigid filament  $0.16$  mm long at one pole and another  $0.2$  mm long at the other pole. Vitellaria co-extensive with intestinal branches; vitelline reservoir Y-shaped, nearly midventral; its arms widely divergent, each connected with seminal receptacle of its own side. Paired seminal receptacles elongate fusiform,  $0.2\text{--}0.43$  mm long, containing abundant yolk cells and sperm, situated one on each side of ovary at level of junction of middle with posterior third of body. Vaginae symmetrical, funnel-shaped at base, opening ventrolaterally by a small round pore at a distance of  $0.4\text{--}1.2$  mm from head end; the vaginal duct arising from the bottom of the vaginal funnel proceeds medioposteriad to unite with its fellow of the other side, the resulting unpaired median duct runs backward and apparently empties into the vitelline reservoir at junction of the two arms. It is worth while to note that sperm are seen scattered in various parts of the vitelline ducts. This fact may be accounted for by the presence of paired seminal receptacles connected with the arms of the Y-shaped vitelline reservoir.

**DISCUSSION:** Although this genus differs markedly from *Pseudodidiclidophora* (loc. cit.) in general body shape, it agrees completely with the latter in the most important characters such as clamp structure and internal anatomy, particularly in possessing paired receptaculum seminis vitellariorum. The presence of a long anchor-bearing caudal appendage, however, prevents its being assigned to the same genus. I would rather consider this character combined with the symmetrical arrangement of the opisthohaptor clamps to be of subfamily importance, hence a new subfamily Allopseudodidiclidophorinae is proposed.

#### Allopseudodidiclidophorinae, n. subf.

**SUBFAMILY DIAGNOSIS:** Pseudodidiclidophoridae: Opisthohaptor symmetrical, with 4 pairs of

FIG. 9. *Allopseudodidiclidophora opelu* n. g., n. sp. 9A, Holotype, ventral view; 9B, clamp, ventral view; 9C-E, caudal anchors; 9F, male terminal genitalia, ventral view.



clamps along posterior border of body, with a long anchor-bearing caudal appendage. Intestinal limbs united together at posterior end of body proper.

*Allopseudodiclidophora* n. g.

GENERIC DIAGNOSIS: Pseudodiclidophoridae, Allopseudodiclidophorinae: Body markedly attenuated anteriorly. Clamps sessile, 4 on each side on posterior margin of body, arranged symmetrically; clamp skeleton similar to that of *Pseudodiclidophora*. Prohaptoral suckers aseptate, unspined. Esophagus very long, simple. Intestinal crura united posteriorly. Testes numerous, in two longitudinal rows in postovarian interintestinal field. Cirrus forming sclerotized cylinder, opening into genital atrium, latter with outer wall of circular muscle fibers and provided inside with a sheaf of sclerotized rods surrounding cirrus. Genital pore midventral, far anterior to intestinal bifurcation. Ovary inverted U-shaped, in midregion of body, with both ends directed backwards. Genito-intestinal duct opening into right intestinal limb. Symmetrical seminal receptacles connected with both arms of vitelline reservoir. Eggs with polar filament. Vaginae symmetrical, vaginal ducts united together; unpaired median vaginal duct opening into vitelline reservoir. Vitellaria co-extensive with intestinal branches; vitelline reservoir Y-shaped. Gill parasites of marine teleosts.

TYPE SPECIES: *A. opelu* n. sp., on *Decapterus pinnulatus*; Hawaii.

10. *Pseudopisthogyne lepidocybii* n. g., n. sp.

Fig. 10

HABITAT: Gill of *Lepidocybium flavobrunneum*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 10.

DESCRIPTION (based on seven whole mounts): Body elongate, rather slender, gradually tapering anteriorly, 4.3–13.5 mm in total length including slender, hook-bearing caudal appendage which arises from the extreme posterior end of the body proper nearer to the small posteriormost clamp than to large posteriormost clamp, and measures 0.4–1.4 mm long and 0.07–0.18 mm wide at the slightly enlarged, truncate tip. Of the three pairs of anchors the largest outer

is 51–64 $\mu$  long from end of short root to height of curve of blade, with prominent guard curved toward the blade, the middle 18–26 $\mu$  long, with its incurved guard well apart from tip of root; the inner 27–31 $\mu$  long, its guard to which many muscle bundles are convergently attached is directed straight toward the tip of the blade. Opisthohaptor asymmetrical, with four pairs of clamps, 0.34–0.9 mm long on the right (pore side), 0.7–2.5 mm long on the left; right clamps distinctly pedunculate, left ones subsessile; skeleton of right clamp 90–160 $\mu$  in diameter, symmetrical, or only slightly asymmetrical because of different curvature of the lateral sclerites, consisting of median spring with bifid ends, a pair of accessory sclerites, two pairs of unjointed lateral arms and a pair of short basal sclerites; skeleton of left clamp 150–330 $\mu$  wide, consisting of two pairs of asymmetrical unjointed lateral arms, a median spring with bifid ends, a pair of accessory sclerites and a pair of basal sclerites; capsule of the clamp strongly muscular; proximal outer quadrant distinctly larger than proximal inner quadrant, bulging out at base, thus causing asymmetry of the lateral sclerites; the two lateral sclerites of the proximal outer quadrant showing gentle sigmoid curve in strong contrast with the opposite sclerites which are simply arcuate. Head blunt-pointed, 0.17–0.28 mm wide at level of oral aperture, with a pair of well-developed apical organs. Intrabuccal sucker elliptical, muscular, with a partition at middle, 50–90  $\times$  70–140 $\mu$ . Pharynx subglobular, cellular, 40–80  $\times$  40–70 $\mu$ . Esophagus 0.22–0.63 mm long, simple except at its diverticulate posterior portion, bifurcating at level of vagina. Intestinal limbs with numerous subdivided outer branches, terminating close to each other at base of caudal appendage.

Testes rounded, 90–170 in number, arranged in one layer, occupying whole interintestinal field of posterior part of anterior third and entire middle third of body. Vas deferens winding between two rows of anteriormost testes and also in pretesticular interintestinal field where there are numerous gland cells surrounding the vas deferens. Whether these gland cells are prostatic in nature or not is not certain. After passing dorsal to the vaginal pore it forms a

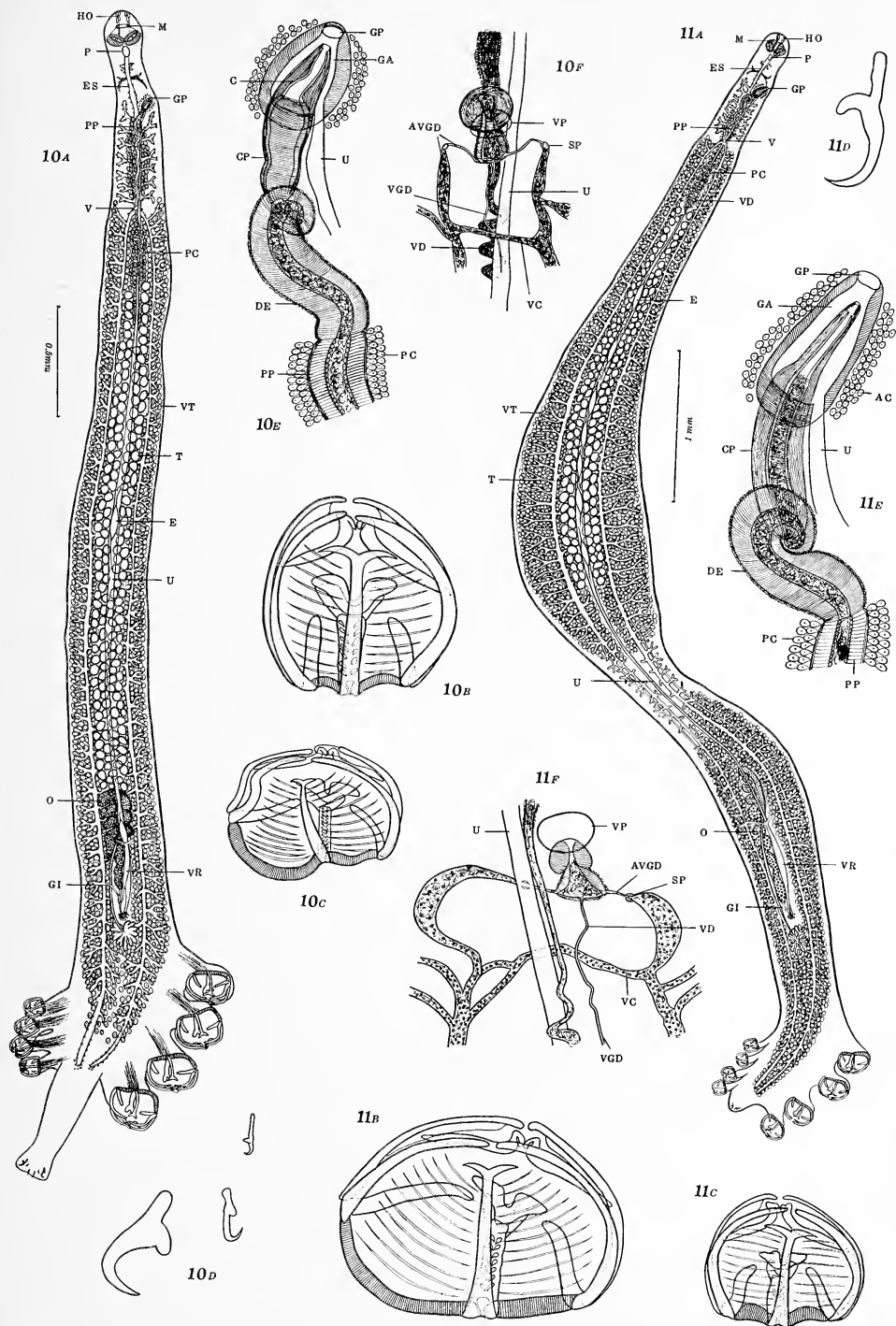


FIG. 10. *Pseudopisthogyne lepidocybii* n. g., n. sp. 10A, Holotype, ventral view; 10B-C, clamps, ventral view; 10D, caudal anchors; 10E, terminal genitalia, ventral view; 10F, vagina and its ducts, ventral view.

FIG. 11. *Allopseudopisthogyne constricta* n. g., n. sp. 11A, Holotype, ventral view; 11B-C, clamps; 11D, caudal anchor; 11E, terminal genitalia, ventral view; 11F, vagina and its duct, ventral view.

somewhat muscular sigmoid duct and leads into slightly winding pars prostatica 0.2–0.5 mm long and provided with circular muscle fibers and a coat of prostatic cells; ejaculatory duct sigmoid, 0.1–0.22 mm long, with a very thick coat of circular muscle fibers, with its anterior end usually turned back on itself to lead into cirrus pouch. Latter cylindrical, 0.12–0.26 mm long by  $30\text{--}55\mu$  wide, with longitudinal muscles, projecting into genital atrium which consists mainly of circular muscle fibers. Immediately outside this genital atrium and cirrus pouch there is a thick coat of accompanying cells. Common genital pore on sinistroventral margin of body 0.35–0.8 mm from head end.

Ovary  $0.5\text{--}1.15 \times 0.08\text{--}0.22$  mm, occupying interintestinal field at anterior half of caudal third of body, consisting of multilobed proximal end situated posteriorly, a narrow tubular portion ascending medial to right intestinal limb, and a looped main portion situated anteriorly with distal end directed posteriad. Germiduct running straight backward from distal end of ovary, giving off narrow genito-intestinal duct just before joining vitelline reservoir; ootype just anterior to proximal lobe of ovary. Uterus midventral, finally running alongside muscular ejaculatory duct and cirrus pouch and opening into genital atrium. Eggs fusiform, 0.2–0.21 mm long, with rather rigid bipolar filament 0.18–0.28 mm long. Vagina provided with sphincter-like circular muscles, with wide midventral opening at a distance of 0.8–1.9 mm from head end. Accessory vaginal ducts arising sideways, one on each side of vagina, each provided with sphincter-like circular muscle fibers at the point where it turns backwards to join the transverse commissure between anastomosing anteriormost vitelline ducts of two sides; median vaginal duct proper arising from middle of base of vagina traceable some distance back of vagina, but its posterior termination not determined. Vitellaria co-extensive with intestine; vitelline reservoir Y-shaped, with long stem co-inciding with ovarian zone.

DISCUSSION: This genus grossly agrees with *Opisthogyne* Unnithan, 1962, in general anatomy, but differs in several important characters such as: (1) oblique body ridges, as observed in *Opisthogyne* and *Gemmacaputia*, are entirely

absent; (2) marked asymmetry of opisthohaptor; (3) subsessile clamps with asymmetrical lateral sclerites due to unequal development of capsule of one proximal quadrant, whereas pedunculate clamps are symmetrical in skeleton; (4) ovarian complex shifted far backward by enormous number of testes; (5) vaginal pore midventral instead of middorsal. These differences, especially the asymmetrical opisthohaptor, the asymmetrical skeleton of subsessile clamps, and absence of oblique body ridges, are sufficient to justify the erection of a separate genus, for which *Pseudopisthogyne* is suggested in recognition of its marked resemblance to *Opisthogyne* Unnithan, 1962. In *Opisthogyne* Unnithan states that the vaginal duct opens into the ootype, but this is obviously an error.

### *Pseudopisthogyne* n. g.

GENERIC DIAGNOSIS: Discocotylidae, Opisthogyninae. Body elongate, nearly symmetrical, without oblique body ridges posteriorly. Opisthohaptor asymmetrical, with four larger subsessile clamps on pore side, and four smaller pedunculate clamps on antiporal side; larger clamp with asymmetrical basal and lateral sclerites, smaller clamp with exactly or nearly symmetrical lateral sclerites. Caudal appendage with three pairs of anchors, attached to posterior end of body between posteriormost clamps of two sides nearer to small clamp than to large clamp. Head blunt-pointed, with well-developed paired apical organs. Esophagus diverticulate posteriorly, bifurcating at level of vagina; intestinal limbs not confluent posteriorly. Testes very numerous, preovarian; pars prostatica, ejaculatory duct, cirrus pouch and genital atrium well differentiated; cirrus unarmed. Common genital pore in esophageal zone, ventrosubmarginal. Ovary turned back on itself, posterior, with both ends directed backward. Eggs fusiform, with bipolar filaments. Vagina midventral, far posterior to genital pore, with paired accessory vaginal ducts, each of which is connected with the transverse commissure between the anterior anastomosing vitelline ducts of the two sides, median vaginal duct proper rudimentary. Vitellaria co-extensive with intestine; vitelline reservoir Y-shaped, in ovarian zone; anterior vitelline ducts containing sperm. Gill parasites of marine teleosts.



TYPE SPECIES: *P. lepidocybii* n. sp., on *Lepidocybium flavobrunneum*; Hawaii.

11. *Allopseudopisthogyne constricta* n. g., n. sp.

Fig. 11

HABITAT: Gill of *Lepidocybium flavobrunneum*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 11.

DESCRIPTION (based on 20 whole mounts): Body elongate, 7.6–16.5 mm long by 0.8–1.6 mm, gently curved in widest testicular region to the left, but to the right posterior to region of body constriction which usually occurs behind the midregion of the body. Opisthaptor asymmetrical, with four larger sessile clamps on pore side and four smaller pedunculate clamps on other side. Skeleton of small clamps 90–130  $\mu$  wide, consisting of two pairs of symmetrical lateral sclerites, a pair of accessory sclerites, a pair of basal sclerites and a median spring with anchor-shaped tip for longer prong and V-shaped winglike apical piece for bifid end of shorter fenestrated prong. Skeleton of left larger clamp 190–270  $\mu$  wide, consisting of two pairs of asymmetrical lateral sclerites, a pair of accessory sclerites, a pair of basal sclerites, and a median spring with anchor-shaped tip for longer prong and V-shaped apical piece for bifid end of shorter fenestrated prong; the proximal outer quadrant of the clamp capsule is a little larger than the corresponding inner quadrant, thus causing asymmetry of lateral and basal sclerites which is, however, not so pronounced as in *Pseudopisthogyne*, in which the two lateral sclerites of the proximal outer quadrant show a gentle sigmoid curve. At the extreme posterior end of the body nearer to the small clamp than to the large clamp is a conical appendage 0.1–0.17 mm long and bearing a pair of hooks close to its rounded or truncate apex; this hook is 46–54  $\mu$  long from tip of root to height of curve of blade, with a very prominent guard curved toward the blade.

Head rounded at apex, 0.19–0.44 mm wide at level of ventral mouth aperture; apical gland complex present as in *Pseudopisthogyne* and *Pseudopisthogyneopsis*. Paired oral suckers elliptical, 60–100  $\times$  90–140  $\mu$ , with a median septum.

Pharynx small, containing cellular element only, 60–80  $\times$  40–70  $\mu$ . Esophagus nearly simple anteriorly but sending posteriorly a number of lateral branches at right angles, bifurcating dorsal to vagina. Intestinal limbs with few simple or ramified side branches and not accompanied by vitellaria in constricted region; in the region of the opisthaptor the side branches are markedly reduced and the limbs run parallel to each other in the median field, being surrounded by vitellaria, and terminate near the base of the hook-bearing caudal appendage.

Testes rounded, 120–185 in number, extending in 2–4 longitudinal rows in interintestinal field from about middle of anterior third to equatorial level far away from ovary and never reaching to it in strong contrast with those of *Pseudopisthogyne* and *Pseudopisthogyneopsis*. Vas deferens markedly winding between anteriormost testes and intestinal bifurcation, surrounded by prostate-like gland cells; in the region of the vaginal pore it forms a sigmoid muscular canal and leads into the pars prostatica a little anterior to the vaginal pore. Pars prostatica undulating, muscular, median, 0.16–0.5 mm long, surrounded throughout its length by numerous prostate cells. Ductus ejaculatorius cylindrical, 0.16–0.25 mm long, up to 50  $\mu$  wide, provided with a thick layer of circular muscles, usually with its anterior end turned back on itself before leading into cirrus. Cirrus simple, narrow, unarmed, enclosed in a cylindrical pouch of longitudinal muscles 0.11–0.23 mm long by 25–50  $\mu$  wide. Genital atrium consisting mainly of circular muscle fibers and surrounded by numerous accompanying cells, enclosing distal portion of cirrus pouch, cirrus and uterus. Common genital pore ventrosubmarginal, 0.38–0.7 mm from head end.

Ovary 0.9–1.8  $\times$  0.12–0.25 mm, composed of branched proximal lobe situated near posterior end of body proper, a long, tubular, ascending portion, and a winding, looped, distal portion, from the rather straight, descending, terminal portion of which arises the germiduct. Genito-intestinal duct opening into right intestinal limb anterior to distal end of ovary. Shell gland complex just anterior to branched proximal lobe of ovary. Uterus midventral except for its terminal portion running alongside cirrus pouch. Eggs

fusiform, 0.2–0.26 mm long, 60–90 $\mu$  wide; bipolar filament 0.25–0.32 mm long. Vagina opening midventrally at a distance of 0.82–1.55 mm from head end, provided with a bulb of circular muscles near its comparatively wide, circular aperture; paired accessory vaginal duct arising sideways from base of vagina, running transversely and then turning backward to join transverse commissure between anastomosing anteriormost vitelline ducts of two sides; median vaginal duct proper can be traced further back of this commissure, but its posterior termination is unknown. Vitellaria commencing in lateral fields at level of vaginal pore, confluent in post-ovarian region; vitelline reservoir Y-shaped with its stem between ovary and left intestinal limb.

DISCUSSION: This genus differs from the most closely related *Pseudopisthogyne* in the body being distinctly constricted posterior to the widest midregion, in the ovary being widely separated from the testes by this constricted area, and in the caudal appendage being reduced to a conical process bearing only one pair of hooks. That the lateral sclerites of the larger clamps do not show a sigmoid curve in contrast with those of *Pseudopisthogyne* or *Pseudopisthogynopsis* is also worth noting.

### *Allospseudopisthogyne* n. g.

GENERIC DIAGNOSIS: Discocotyliidae, Opisthogyninae: Body elongate, asymmetrical, constricted a little posterior to widest midregion, without oblique body ridges posteriorly. Opisthohaptor asymmetrical, with four large subsessile clamps on side of genital pore and four smaller pedunculate clamps on other side; larger clamp with asymmetrical basal and lateral sclerites, latter sclerites not showing sigmoid curve; smaller clamp with exactly symmetrical lateral sclerites. Caudal appendage reduced to conical process, with only one pair of hooks, attached to posterior end of body nearer to small clamp than to large clamp. Head blunt-pointed, with apical organs. Esophagus bifurcating at level of vaginal pore; intestinal limbs with side branches, not accompanied by vitellaria in constricted part of body, not confluent posteriorly. Testes very numerous, widely separated from ovary by body constriction. Pars prostatica, ejaculatory duct, cirrus pouch and genital atrium well differen-

tiated just as in *Pseudopisthogyne* and *Pseudopisthogynopsis*. Cirrus unarmed. Common genital pore in esophageal zone, ventrosubmarginal. Ovary turned back on itself in posterior third of body, with both ends directed backwards. Eggs fusiform, with bipolar filaments. Vagina provided with sphincter, opening midventrally far posterior to common genital pore, at intestinal bifurcation; paired accessory vaginal ducts connected with transverse commissures between anteriormost anastomosing vitelline ducts of two sides; median vaginal duct proper rudimentary. Vitellaria co-extensive with intestine except at constricted part of body, confluent posterior to ovary; vitelline reservoir Y-shaped, sinistral to ovary; anterior vitelline ducts containing sperm. Gill parasites of marine teleosts.

TYPE SPECIES: *A. constricta* n. sp., on *Lepidocybium flavobrunneum*; Hawaii.

### 12. *Pseudopisthogynopsis lepidocybii* n. g., n. sp.

Fig. 12

HABITAT: Gill of *Lepidocybium flavobrunneum*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 12.

DESCRIPTION (based on 50 whole mounts): Body elongate, 15–13 mm long, 0.55–1.4 mm wide just in front of opisthohaptor, tapering anteriorly, symmetrical except for posterior end, to which four larger subsessile clamps are attached on the side of the genital pore and four smaller pedunculate clamps on the other side, without hook-bearing appendage between two posteriormost clamps. Skeleton of small clamp 100–170 $\mu$  wide, consisting of two pairs of symmetrical or slightly asymmetrical, unjointed, lateral sclerites, a median spring with bifid ends of which the shorter prong has a V-shaped apical piece, a pair of accessory sclerites and a pair of short basal sclerites; skeleton of larger clamp 280–420 $\mu$  wide at base, consisting of two pairs of distinctly asymmetrical, unjointed, lateral sclerites, a median spring with bifid ends, a pair of accessory sclerites and a pair of basal sclerites. On the tip of the shorter, fenestrated prong of the median spring is set a V-shaped, more weakly sclerotized, apical piece. The capsule of the larger clamp is more muscular than that of the smaller



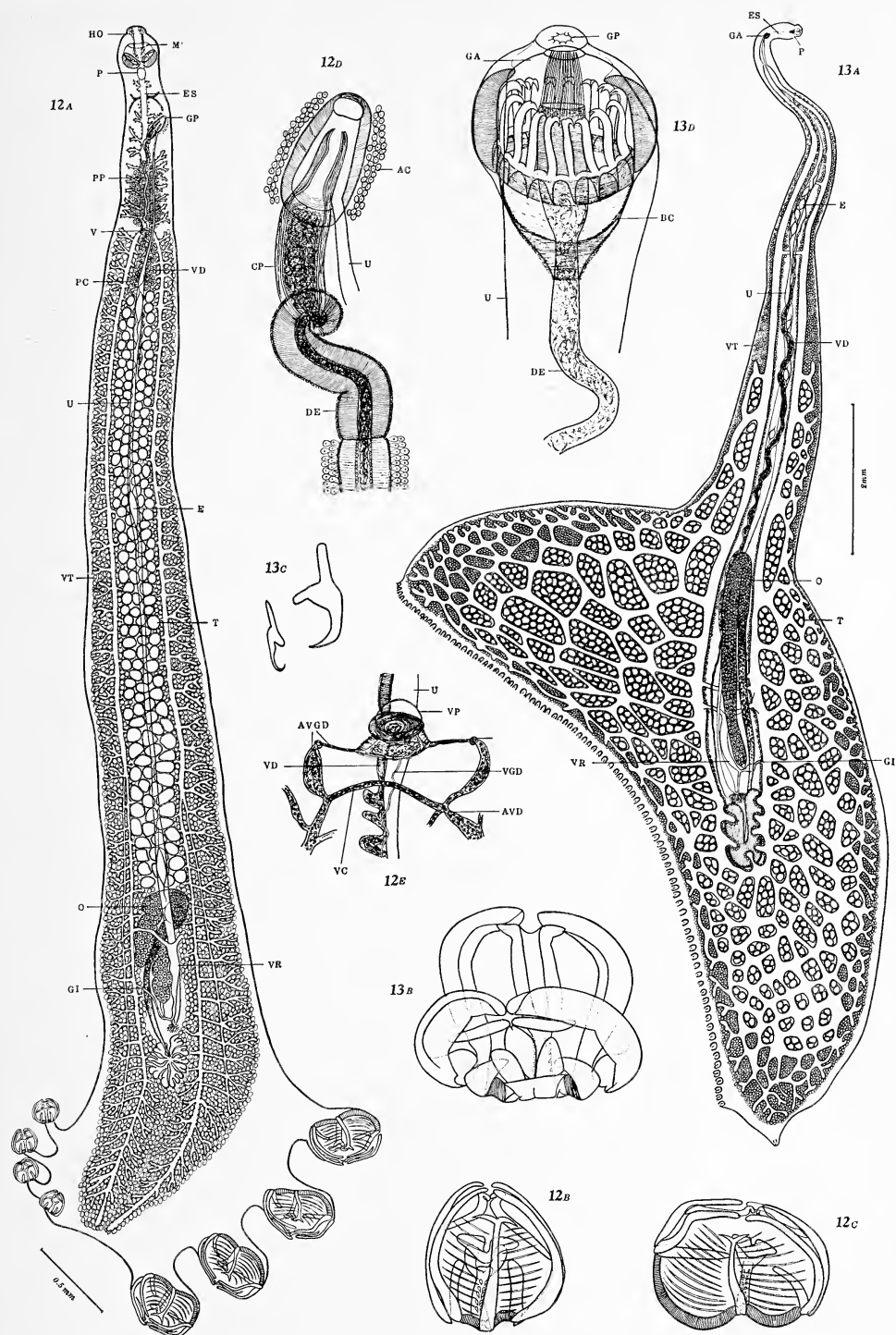


FIG. 12. *Pseudopisthogynopsis lepidocybii* n. g., n. sp. 12A, Holotype, ventral view; 12B-C, clamps; 12D, terminal genitalia, ventral view; 12E, vagina and its ducts, ventral view.

FIG. 13. *Areotestis sibi* n. g., n. sp. 13A, Holotype, dorsal view; 13B, clamp, dorsal view; 13C, caudal anchors; 13D, terminal genitalia, ventral view.

clamp, and its proximal outer quadrant is so much developed as to push the lateral and basal sclerites of its own side toward the apex of the clamp, thus causing asymmetry of the clamp skeleton; the lateral sclerites of the proximal outer quadrant showing a gentle sigmoid curve in contrast with opposite lateral sclerites.

Head blunt-pointed, 0.2–0.42 mm wide at level of ventral mouth aperture, with a pair of well-developed apical organs. Oral suckers elliptical,  $0.06\text{--}0.11 \times 0.1\text{--}0.18$  mm, with a septum at middle. Pharynx not muscular,  $40\text{--}90 \times 30\text{--}70\mu$ ; esophagus distinctly diverticulate posteriorly, 0.2–0.7 mm long, surrounded by pigment cells, bifurcating at level of vagina. Numerous outer intestinal branches extend outward through the very dense layer of vitellaria up to the very lateral margin of the body. In the postovarian area the intestinal limbs are close to each other and terminate near the extreme posterior end of the body.

Testes rounded, 90–185 in number, occupying whole interintestinal field in posterior half of anterior third and entire middle third of body, between vas deferens coils and ovary, in two longitudinal rows anteriorly and four zigzag rows posteriorly. Vas deferens winding first between two rows of anteriormost testes and then in postbifurcal interintestinal area, where it is surrounded by numerous prostate-like cells. From a little anterior to the vaginal pore extends forwards in the median field a slightly winding muscular pars prostatica 0.22–0.6 mm long by  $30\text{--}65\mu$  wide and surrounded by numerous prostate cells; it passes into the strongly muscular ejaculatory duct which is 0.1–0.25 mm long by  $30\text{--}60\mu$  wide and usually turns back on itself at its anterior end to be continued into the cirrus. Cirrus simple, unarmed, enclosed in cylindrical, muscular, cirrus pouch. Latter 0.16–0.25 mm long,  $40\text{--}60\mu$  wide, provided with longitudinal muscle fibers, extending obliquely toward left margin of body. Genital atrium  $93\mu$  wide in the type, surrounded by accompanying cells, provided with circular muscles, opening ventrosubmarginally at a distance of 0.44–1.0 mm from head end.

Ovary longitudinally elongated, shaped like an 8, situated in anterior half of caudal third of body, with both ends directed backwards,  $0.9\text{--}$

$2.3 \times 0.12\text{--}0.3$  mm; proximal part multilobulated in a rosette-shape, next ascending portion tubular, crossing descending distal portion dorsally; descending distal portion winding backward medial to right intestinal limb and then medial to ascending tubular portion. Genito-intestinal duct provided with circular muscle fibers, arising from germiduct just in front of junction of germiduct with stem of vitelline reservoir, opening into right intestinal limb at level of distal end of ovary. Shell gland cells massed closely together anterior to rosette-shaped portion of ovary. Uterus midventral, opening into genital atrium alongside cirrus pouch on its posteroventral side. Eggs elliptical,  $0.22\text{--}0.25$  mm long by  $50\text{--}70\mu$  wide; bipolar filament rather rigid, 0.2–0.35 mm long. Vagina surrounded by lamellae of circular muscle fibers like a sphincter, opening midventrally at a distance of 0.95–2.2 mm from head end; paired accessory vaginal ducts arising sideways from base of vagina, first running transversely, turning backward at the point provided with sphincter-like circular muscle fibers, may be distended with sperm together with yolk cells before uniting with transverse commissure of anastomosing anteriormost vitelline ducts; median vaginal duct proper traceable in median field for some distance back of vagina, but its posterior termination not determined. Vitellaria extending in lateral fields, commencing at level of vaginal pore, confluent in postovarian median field; vitelline reservoir Y-shaped; longer right arm crossing swollen distal portion of ovary on its ventral side; stem long, descending on left side of terminal descending portion of ovary.

DISCUSSION: This genus differs from *Pseudopisthogyne* only in the absence of the hook-bearing caudal appendage. It is defined as follows:

*Pseudopisthogynopsis* n. g.

GENERIC DIAGNOSIS: Discocotyliidae, Opisthogyninae: Body elongate, nearly symmetrical, without oblique body ridges posteriorly. Hook-bearing caudal appendage absent. Opisthohaptor asymmetrical, with four larger sessile clamps on side of genital pore and four smaller pedunculate clamps on other side; larger clamp with asymmetrical, basal and lateral sclerites, smaller clamps with exactly or nearly symmetrical lat-

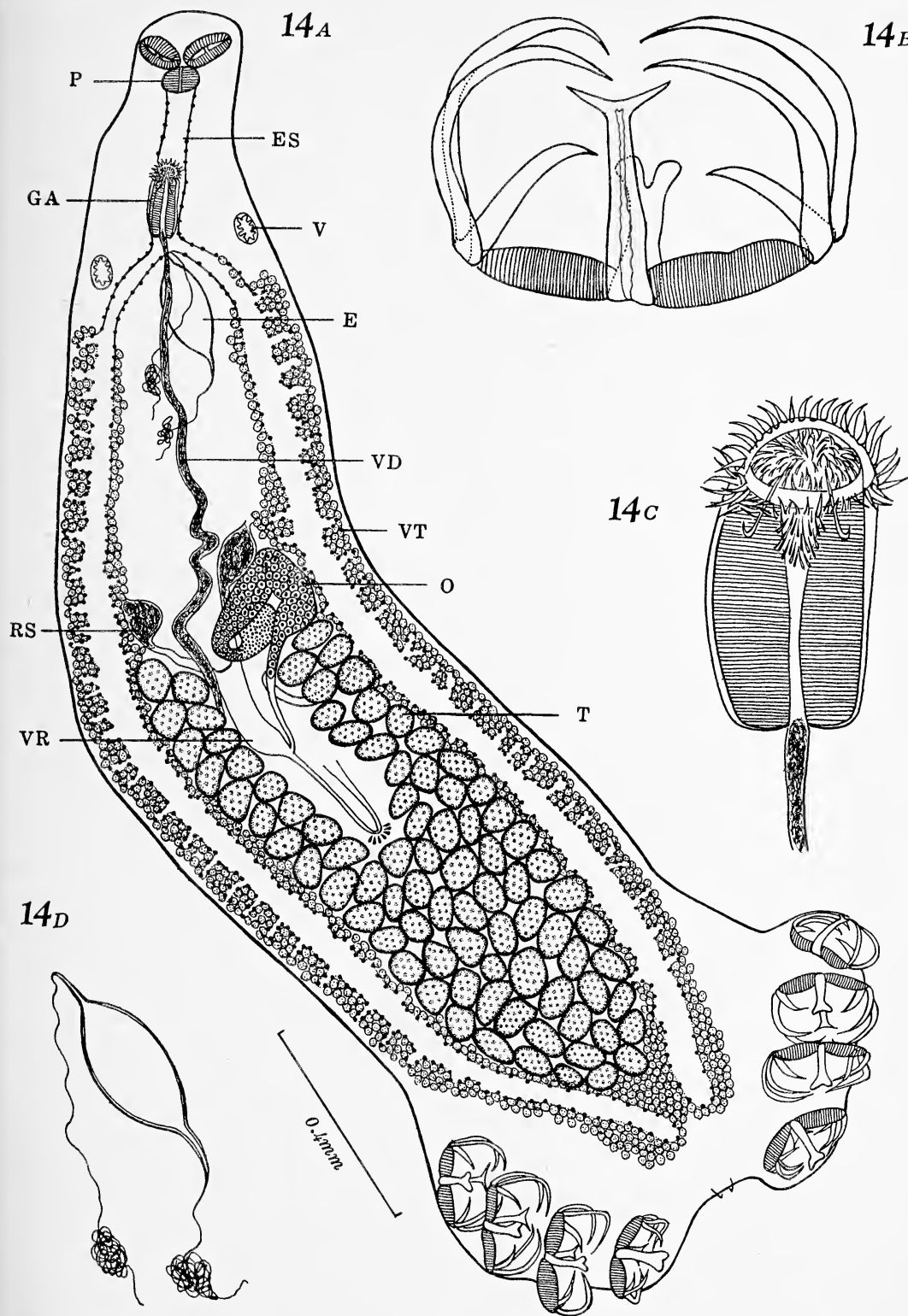


FIG. 14. *Pseudodiscocotyla opakapaka* n. g., n. sp. 14A, Holotype, dorsal view; 14B, clamp; 14C, male terminalia, ventral view; 14D, egg.

eral sclerites. Head blunt-pointed, with well-developed paired apical organs. Esophagus bifurcating at level of vagina; intestinal limbs not confluent posteriorly. Testes very numerous, preovarian; vas deferens winding and surrounded by numerous prostate-like gland cells in postvaginal median field; prostatic complex, muscular ejaculatory duct, cirrus pouch and genital atrium well differentiated. Cirrus unarmed. Common genital pore ventrosubmarginal, anterior. Ovary posterior, turned back on itself, with both ends directed backwards. Eggs fusiform, with bipolar filaments. Vagina simple, surrounded by circular muscle fibers in form of a sphincter, with midventral opening far posterior to genital pore; paired accessory vaginal ducts connected with transverse commissure of anteriormost anastomosing vitelline ducts, median vaginal duct proper rudimentary. Vitellaria co-extensive with intestine, confluent posteriorly; vitelline reservoir Y-shaped, to left of ovary; anterior vitelline ducts containing sperm. Gill parasites of marine teleosts.

TYPE SPECIES: *P. lepidocybii* n. sp. on *Lepidocybium flavobrunneum*; Hawaii.

13. *Pseudodiscocotyla opakapaka* n. g., n. sp.  
Fig. 14

HABITAT: Gill of *Pristipomoides microlepis* (local name "opakapaka") and *Aphareus rutilans*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 13.

DESCRIPTION (based on 20 whole mounts): Body tapering anteriorly, 1.6–2.7 mm in length, with maximum width of 0.22–0.6 mm at posterior half of body. Opisthohaptor with a median pair of larval hooklets at posterior end, divided into symmetrical lobes, each bearing an oblique row of four subequal clamps; clamp skeleton 0.1–0.18 mm wide, consisting of a dorsal and a ventral pair of slender, unjointed, lateral arms, a median spring with bifid ends, and a pair of incurved basal rods. Head truncate, 0.15–0.2 mm wide. Paired oral suckers septate, 40–70 × 60–110 $\mu$ . Pharynx pyriform, 30–60 × 30–45 $\mu$ . Esophagus short, bifurcating just behind bulbus cirri. Ceca with short inconspicuous diverticles, extending into opisthohaptor, terminating very close to each other near wide posterior sinus between two lobes of opisthohaptor.

Testes 50–100 in number, occupying nearly whole postovarian intercecal field, divided into two lateral groups from behind ovary to level of shell gland. Vas deferens winding in median field dorsal to uterus. A stout ellipsoidal bulbus cirri about 75 × 60 $\mu$ , provided subapically with a median group of 12 minute acicular spines and a pair of longer, very slender, lateral spicules, and apically with a certain number of slightly curved spines massed together; genital atrium with a crown of two alternating rows of minute spines, opening midventrally at a distance of 0.17–0.35 mm from head end.

Ovary bent back on itself, with its distal end directed backward, 100–170 × 60–112 $\mu$ , situated on the right of median line just in front of middle of body. Germiduct arising from ovary soon gives off genito-intestinal duct opening into right intestine, and after joining the vitelline reservoir continues its backward course between the two submedian groups of testes, and then turns forward to be surrounded by shell gland cells. Uterus midventral, strongly distended with eggs in some specimens. Eggs elliptical, 160–180 × 60–70 $\mu$ , with a very long, fine, convoluted filament at each pole. On the ventrolateral surface of the body at a distance of 0.27–0.45 mm from the head end there is a pair of oval symmetrical vaginae lined with corrugated cuticle, but their vaginal ducts could not be made out. Vitellaria commencing behind vaginae, and extending along whole length of intestine except for its anteriormost portion; vitelline reservoir Y-shaped, median, with its arms at level of ovary and its stem between two submedian groups of testes. It is very remarkable that each arm is distended with sperm at its anterior end in the form of an oval sac.

DISCUSSION: This genus resembles *Discocotyle* Diesing, 1850, in general anatomy, but differs from it in the intestinal limbs not uniting posteriorly, in the heavily armed bulbus cirri and armed genital atrium, etc. It obviously belongs to Discocotylidae Price, 1936, but cannot be assigned to any known subfamilies, hence a new subfamily is proposed for its reception.

*Pseudodiscotylinae* n. subf.

SUBFAMILY DIAGNOSIS: Discocotylidae. Terminal anchor-bearing lappet absent. Haptoral

clamps of four pairs, subequal, of *Discocotyle* type, bivalved, sessile. Vagina double.

*Pseudodiscocotyla* n. g.

GENERIC DIAGNOSIS: Discocotylidae, Pseudodiscocotylinae. Body tapering anteriorly; opisthohaptor two-lobed, with a median pair of larval hooklets posteriorly and four pairs of subequal bivalved clamps; clamp skeleton consisting of two pairs of slender, unjointed, lateral arms, a median spring and a pair of incurved basal rods. Prohaptor oral sucker septate. Esophagus bifurcating posterior to genital pore; ceca slightly diverticulate, not united posteriorly. Testes very numerous, occupying nearly whole postovarian intercecal field. Armed bulbus cirri present. Genital atrium armed. Genital pore prebifurcal. Ovary turned back on itself, with its distal end directed backwards. Genito-intestinal duct present. Shell gland complex between two submedian groups of testes. Eggs elliptical, large, with convoluted filament at each pole. Vaginae lined with corrugated cuticle, situated ventrally near lateral margins of body at a level a little behind genital pore; vaginal duct not traced. Vitellaria extending along entire intestinal limbs posterior to vaginae; vitelline reservoir Y-shaped, with its arms distended with sperm at its anterior end in form of oval sac. Gill parasites of marine teleosts.

TYPE SPECIES: *P. opakapaka* n. sp. on gills of *Pristipomoides microlopis* and *Aphareus rutilans*; Hawaii.

14. *Allopseudaxinoides euthynni* n. g., n. sp.

Fig. 15

HABITAT: Gills of *Euthynnus yaito* (local name "kawakawa"); Hawaii.

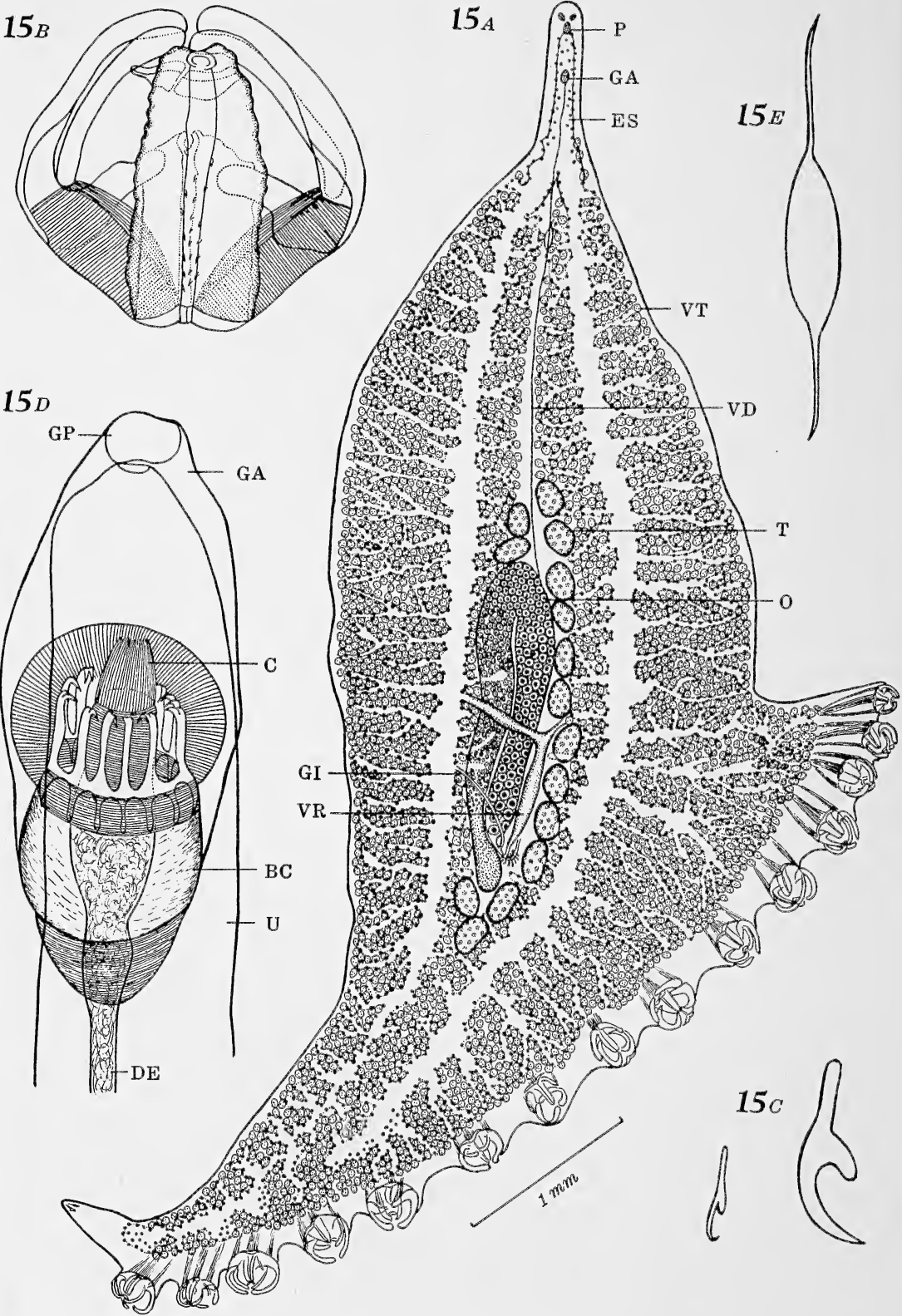
HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 14.

DESCRIPTION (based on 12 whole mounts): Body large, 5–8 mm long from head end to tip of caudal appendage, markedly tapered in head and esophageal regions, widest (2.9–5.5 mm) at opisthohaptor which extends obliquely along the posterior end of the body proper. Opisthohaptor unilateral, bearing a row of 13–15 clamps and a prominent digitiform caudal appendage which is provided at its blunt end with two pairs of anchors; outer anchor 47–53 $\mu$  long, inner one 22–25 $\mu$  long. Clamp bivalved, 0.15–

0.3 mm in diameter; median spring U-shaped, with rounded ends, consisting of sclerotized median piece and parallel-sided muscular flange which appears as a winglike lateral extension of the median piece in optical section; the dorsal valve of clamp is supported by a pair of arcuate lateral sclerites meeting at tip of valve and curved medially at base; the ventral valve is supported by a pair of apically slightly curved sclerites meeting in the median line and articulating at the base with the dorsal sclerites at the angle where they bend medially. Beneath the apical ends of the dorsal and ventral sclerites are paired sclerotized thickenings of the median apical margins of the capsules of the dorsal and ventral valves. Head rounded, 0.13–0.17 mm wide; mouth ventroterminal. Paired oral sucker 25–35  $\times$  30–43 $\mu$ ; pharynx pyriform, 40–70  $\times$  30–43 $\mu$ , sometimes protruding into buccal cavity. Esophagus simple, 0.38–1.05 mm long; bifurcating a short distance posterior to genital atrium; intestinal limbs with short inner and longer outer branches, terminating in distal portion of opisthohaptor, the right limb reaching to base of caudal appendage.

Testes up to about 20 in number, irregular in shape, extending in interintestinal field from preovarian area to postovarian area, passing in one row on left side of ovary. Vas deferens narrow, almost straight dorsal to uterus. Cirrus forming a bulb surrounded by fine circular muscle fibers, produced forward into a cuticularized short cylinder tipped with a circular row of delicate spiniform structures which projects into the lumen of the genital atrium. Genital atrium spherical, 42–45 $\mu$  in diameter, with thick wall of radial muscle fibers, armed inside with a corona of over a dozen (14–24?) spines 20–25 $\mu$  long whose bifid tips are curved inwards; these spines are supported at the base by another corona of stumpy denticles. Genital pore midventral, 0.25–0.6 mm from head end.

Ovary 1.3–1.8  $\times$  0.15–0.4 mm, turned back on itself in midregion of body, with both ends directed backwards. Genito-intestinal duct crossing proximal and distal ends of ovary and opening into right intestinal limb. Uterus midventral; eggs elliptical, 0.12–0.2 mm long by 70 $\mu$  wide, with polar filament 0.07–0.14 mm long at each pole. Vitellaria co-extensive with intestine and its branches. Vitelline reservoir Y-shaped; its





stem 0.4–0.6 mm long, and its right arm crossing ovary at about its middle. Vagina entirely lacking.

**DISCUSSION:** This new genus differs from *Allopseudaxine* Yamaguti, 1943, in the complete absence of vaginae and the presence of cuticularized apical thickenings of clamp capsule beneath the apical ends of dorsal and ventral lateral sclerites.

Unnithan (1957) proposed a new genus *Uraxine* which is now regarded as a synonym of *Allopseudaxine* Yamaguti, 1943, and placed it in his new subfamily Monaxiniinae of his family Axinidae. Price (1962) created a new family for *Allopseudaxine*; but I prefer to assign this genus, along with the present new genus, to *Allopseudaxiniinae* Yamaguti, 1963, of Unnithan's Axinidae.

*Allopseudaxinoides* n. g.

**GENERIC DIAGNOSIS:** Axinidae, *Allopseudaxiniinae*. Body large, abruptly tapering anteriorly. Opisthohaptor unilateral, oblique; clamp skeleton consisting of a median U-shaped spring, a pair of dorsal lateral sclerites and a pair of ventral lateral sclerites; ventral lateral sclerite articulating with dorsal lateral sclerite at the angle where the latter turns medially. This pattern of clamp skeleton is exactly similar to that of *Allopseudaxine*, only differing from the latter in having paired sclerotized thickenings at the apex of clamp capsule beneath apex of dorsal and ventral lateral sclerites. Caudal appendage bearing two pairs of anchors. Esophagus bifurcating a short distance posterior to genital pore. Intestinal limbs with numerous side branches, terminating near base of terminal appendage. Testes not very numerous pre-, para-, and postovarian. Genital atrium sucker-like, provided inside with a corona of apically curved spines, at the base of which is another circle of denticles supporting the spines. Ovary tubular, turned back on itself in midregion of body. Eggs elliptical, with filament at each pole. Vaginae absent. Vitellaria co-extensive with intestine and its branches; vitelline reservoir Y-shaped, sinistral to ovary. Parasitic on gills of marine teleosts.

**TYPE SPECIES:** *A. euthynni* n. sp., on *Euthynnus yaito*; Hawaii.

15. *Allomonaxine carangoides* n. g., n. sp.

Fig. 16

**HABITAT:** Gills of *Carangoides* sp.; Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 15.

**DESCRIPTION** (based on 9 whole mounts): Body moderately large, wedge-shaped in outline, tapering anteriorly, widest (0.2–0.27 mm) at the obliquely truncated posterior end, along which is attached a row of 40 to 50 clamps. Clamp skeleton up to 70–110 $\mu$  wide, of *Microcotyle* type, consisting of a U-shaped median piece without accessory apical pieces, two pairs of lateral sclerites and a pair of curved basal rods. Head end truncate, 0.3–0.4 mm wide, with wide ventroterminal mouth aperture. Oral suckers elliptical, septate, 0.08–0.11  $\times$  0.15–0.2 mm. Pharynx pyriform, 57–100  $\times$  47–63 $\mu$ ; esophagus 0.3–0.5 mm long, with few side branches, bifurcating immediately behind genital atrium. Intestinal limbs with numerous, subdivided, outer branches and fewer, simpler, inner branches, not confluent posteriorly; left limb extending beyond right limb to near extreme left end of body.

Testes rounded, very numerous, paved in one layer and occupying whole postovarian interintestinal field; under low power of magnification they appear like a single lobed organ subdivided by inner intestinal branches. Vas deferens winding regularly from one side of median line to the other among inner intestinal branches, convoluted behind intestinal bifurcation. No cirrus differentiated. Genital atrium reniform, 0.16–0.24  $\times$  0.24–0.27 mm, provided with well-developed radial muscle fibers, armed inside with spines of four different types; ventral spines 30–75 $\mu$  long, 34–40 in number, with straight shaft and clawlike point, arranged very close to one another in a transverse row intermingled dorsally at somewhat regular intervals with 14–16 shorter spines whose point is simple and whose shaft is outcurved dorsally about the middle; of the lateral spines four lie transversely on each side at the male genital pore, and 20–22, similar in shape to those longer ventral spines and 50–63 $\mu$  long, are arranged in a gently curved row immediately lateral to the shorter (30–40 $\mu$  long), stouter claw-like, medial

FIG. 15. *Allopseudaxinoides euthynni* n. g., n. sp. 15A, Holotype, ventral view; 15B, clamp, dorsal view; 15C, caudal anchors; 15D, terminal genitalia, ventral view; 15E, egg.

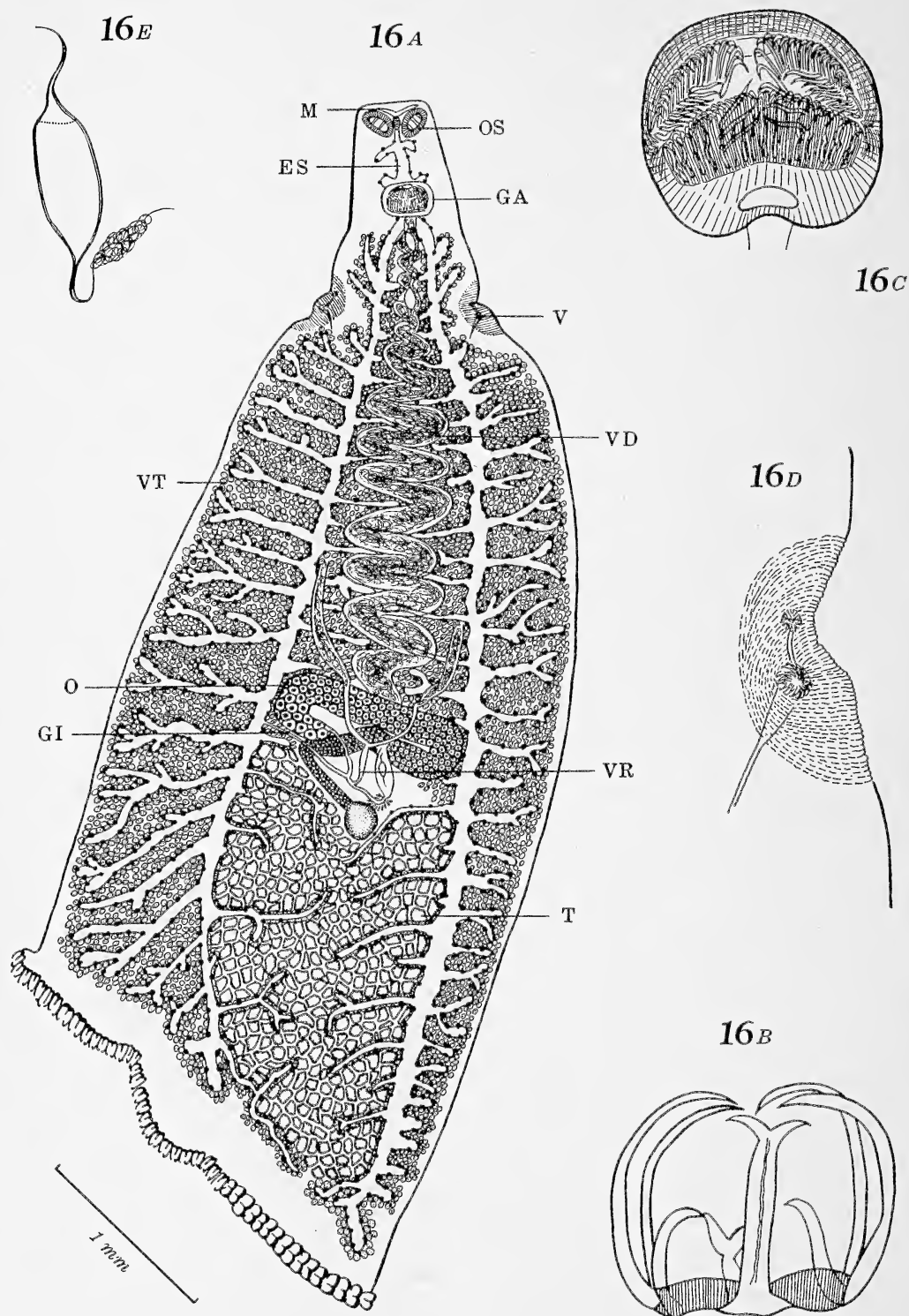


FIG. 16. *Allomonaxine carangoides* n. g., n. sp. 16A, Holotype, ventral view; 16B, clamp, ventral view; 16C, terminal genitalia, dorsal view; 16D, vagina, dorsal view; 16E, egg.



spines which are arranged in a dorsoventral row. Genital pore midventral, prebifurcal, 0.38–0.5 mm from head end.

Ovary equatorial, tubular, originating with or without enlargement, immediately in front of anteriormost testes, describing a double loop, with its distal end directed posteromesad, measuring  $0.5\text{--}0.7 \times 0.6\text{--}0.9$  mm as a whole. Genito-intestinal duct short, opening into right intestinal limb at level of ootype. Uterus midventral; eggs elliptical, about  $0.17 \times 0.07\text{--}0.075$  mm, with long convoluted filament at posterior pole and a shorter, nonconvoluted filament at opercular pole. Vitellaria commencing at a level halfway between intestinal bifurcation and level of vaginae, extending along intestinal branches; vitelline reservoir Y-shaped, overlapping ovary on its ventral side. Vaginae double, dorsolateral, symmetrical, opening a short distance behind intestinal bifurcation, 1.0–1.25 mm from head end; each opening provided densely with acicular spines, surrounded by extremely finely denticulated cuticle, with a conspicuous ventral lateral depression immediately in front; at the bottom of this pit is a mass of over a dozen minute conical teeth representing an accessory vaginal armature. This accessory vagina is connected with the vagina proper by a narrow duct. Vaginal ducts running posteromesad, each probably joining anterior part of collecting vitelline duct of its own side. Longitudinal collecting vitelline duct was seen filled with sperm in one paratype.

DISCUSSION: This genus bears a superficial resemblance to *Monaxine* Unnithan, 1957, but differs fundamentally in the vagina being paired and in having symmetrical, ventrolateral, prevaginal depressions, each of which is provided at the bottom with a small dense mass of conical teeth. These two characters are sufficient to justify the erection of a new genus, for which the name *Allomonaxine* is proposed.

#### *Allomonaxine* n. g.

GENERIC DIAGNOSIS: Axinidae, Monaxininae: Body relatively large, asymmetrically flattened conical. Clamp skeleton of *Microcotyle* type; median spring without apical piece; lateral sclerites unjointed. Esophagus slightly diverticulate; intestinal limbs with inner and other branches, not united posteriorly. Testes very numerous, oc-

cupying whole postovarian interintestinal field. Vas deferens undulating, but convoluted behind intestinal bifurcation. No cirrus differentiated. Genital atrium muscular, armed with spines of different types; genital pore prebifurcal. Ovary in midregion of body, forming a double loop, with its distal end directed posteromesad. No seminal receptacle. Eggs with filament at each pole. Vaginae double, opening dorsolaterally at a short distance posterior to intestinal bifurcation; a prevaginal depression present ventrolaterally, with a small dense mass of conical teeth at its bottom. Each vaginal duct probably opening into anterior part of longitudinal collecting vitelline duct of its own side. Vitellaria commencing a little behind intestinal bifurcation; vitelline reservoir Y-shaped, overlapping ovary. Gill parasites of marine teleosts.

TYPE SPECIES: *A. carangoides* n. sp., on *Carangoides* sp.; Hawaii.

Four specimens similar in structure but definitely smaller in size, from the gill of *Carangoides ferdau* gave the following measurements: Body  $3\text{--}4 \times 1.3\text{--}1.8$  mm with 44–46 clamps; anterior sucker  $40\text{--}60 \times 70\text{--}100\mu$ ; pharynx  $30\text{--}40 \times 30\text{--}38\mu$ ; genital atrium  $0.14\text{--}0.16 \times 0.17\text{--}0.2$  mm, with spines exactly similar in number, size and arrangement to those of *Allomonaxine carangoides*. Vagina  $0.64\text{--}0.8$  mm from head end. Ovary  $0.36\text{--}0.48 \times 0.36\text{--}0.56$  mm. Although the above measurements are entirely different from those of gravid specimens of *Allomonaxine carangoides*, I prefer for the present to regard these four specimens as juvenile forms of this species.

#### 16. *Pseudochaubanea sphyraenae* n. g., n. sp.

Fig. 17

HABITAT: Gill of *Sphyraena barracuda*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 16.

DESCRIPTION (based on five whole mounts): Body lanceolate, tapered anteriorly from level of vagina, usually 4.45–5.8 mm long, but may be up to 10 mm long when completely relaxed, with maximum breadth of 0.32–1.4 mm at posttesticular level. Opisthohaptor without terminal anchors, asymmetrical, without attenuated stalk as seen in *Chaubanea madrasensis* Ramalingam, 1953; clamps unequal, with skeleton of *Gastro-*

*cotyle* type, 28–50 on the right, 25–37 on the left, making a total of 58–87. Paired prohaptor suckers elliptical, muscular, with several septae,  $72-112 \times 37-60\mu$ . Head rounded, truncate at apex, with subterminal mouth opening. Pharynx globular,  $37-58 \times 35-50\mu$ , esophagus 0.83–2.0 mm long, giving off numerous simple or subdivided side branches at right angles, bifurcating just in front of vaginal pore, anteriormost esophageal branches apparently rosette-shaped; intestinal limbs with numerous subdivided branches laterally; each may give off posteriorly two secondary limbs which are also provided with side branches and run backward parallel to the main limbs; these limbs are not accompanied by the vitellaria posteriorly and may or may not reach the posterior end of the opisthohaptor.

Testes rounded, 70–100 in number, pre-, para-, and postovarian, commencing a certain distance (0.5 mm in the type 4.45 mm long) behind vaginal pore, and terminating at level of anteriormost clamp. Distal portion of vas deferens running ventral to esophagus, strongly winding and provided with thick wall of circular muscles. Cirrus pouch fusiform,  $90-160 \times 30-45\mu$ , provided outside with well-developed longitudinal muscles, oblique to body axis on right side of esophagus; cirrus unarmed, opening into relatively wide genital atrium which in turn opens ventrally close to right margin of body at a distance of 0.36–0.84 mm from head end. In the region of the genital pore the body bulges out a little as shown in the figure.

Ovary with irregular outline, confined to middle third of body on right side of median line medial to right intestinal limb, commencing with a compact mass 0.18–0.2 mm wide and ascending for a distance of 0.86–1.4 mm and then descending alongside ascending portion, giving off germiduct just in front of compact proximal mass. The germiduct originating at the posterior distal end of the ovary soon gives off the genito-intestinal duct and then unites with the stem of the vitelline reservoir; the genito-intestinal duct crosses the distal end of the ovary ventrally and empties into the right intestinal limb. Shell gland confined to space between ovary and testes. Uterus midventral, finally running alongside cirrus pouch and opening into genital atrium near its margin. Eggs greatly elongated,  $220-230\mu$  long by  $40\mu$  wide, with

both ends produced into filaments 170–250 $\mu$  long. Vagina bulbous, about 0.11 mm in diameter in the type, opening midventrally just behind intestinal bifurcation, 0.95–2.4 mm from head end; vaginal duct could not be traced backwardly. A pair of narrow symmetrical ducts arising from base of vagina, each provided with a sphincter at distal end, probably united with vitelline duct passing nearby. Vitellaria commencing on each side at level of intestinal bifurcation, leaving posterior ends of intestinal limbs free; vitelline reservoir Y-shaped.

DISCUSSION: The present species differs from *Chaubanea madrasensis* Ramalingam 1953, from *Sphyræna acutipinnis* in the body lacking the haptor stalk, septate anterior suckers, longer esophagus, larger number of testes, and postbifurcal position of the vagina. Ramalingam states that the vagina is lateral on the left side, just beneath and parallel to the short unarmed cirrus, and that the vaginal pore is fringed with minute teethlike spines. This entirely different location of the vagina and the difference in the body shape justify the creation of a new genus, for which the name *Pseudochaubanea* is proposed with the following diagnosis.

*Pseudochaubanea* n. g.

GENERIC DIAGNOSIS: Gastrocorylidae, Gastrocorylinae: Body lanceolate, without stalk for opisthohaptor. Opisthohaptor asymmetrical, not distinctly set off from body proper, with large numbers of clamps of *Gastrocoryle* type; terminal anchors absent. Paired anterior suckers strongly muscular, conspicuously septate; esophagus long, with side branches; ceca also with numerous side branches, continued into opisthohaptor, and terminating separately at or near posterior end of latter where they are not accompanied by the vitellaria. Testes numerous, pre-, para-, and postovarian, passing beside ovary. Vas deferens with thick muscular wall distally; cirrus pouch present; cirrus unarmed, may or may not protrude into genital atrium; genital pore submarginal, in anterior region of esophagus. Ovary in midregion of body, to right of median line, turning back on itself and giving germiduct at its backwardly directed end. Vagina unarmed, opening midventrally, postbifurcal, with paired narrow ducts, each of which probably unites with the vitelline duct passing nearby. Eggs elongate, filamented at both ends.

Vitellaria co-extensive with intestinal limbs except for their posteriormost portion. Gill parasites of marine teleosts.

TYPE SPECIES: *P. sphyraenae* n. sp., on *Sphyraena barracuda*; Hawaii.

17. *Areotestis sibi* n. g., n. sp.

Fig. 13

HABITAT: Gill of *Parathunnus sibi* (type host), *Neothunnus macropterus*, and *Thunnus alalunga*; Hawaii.

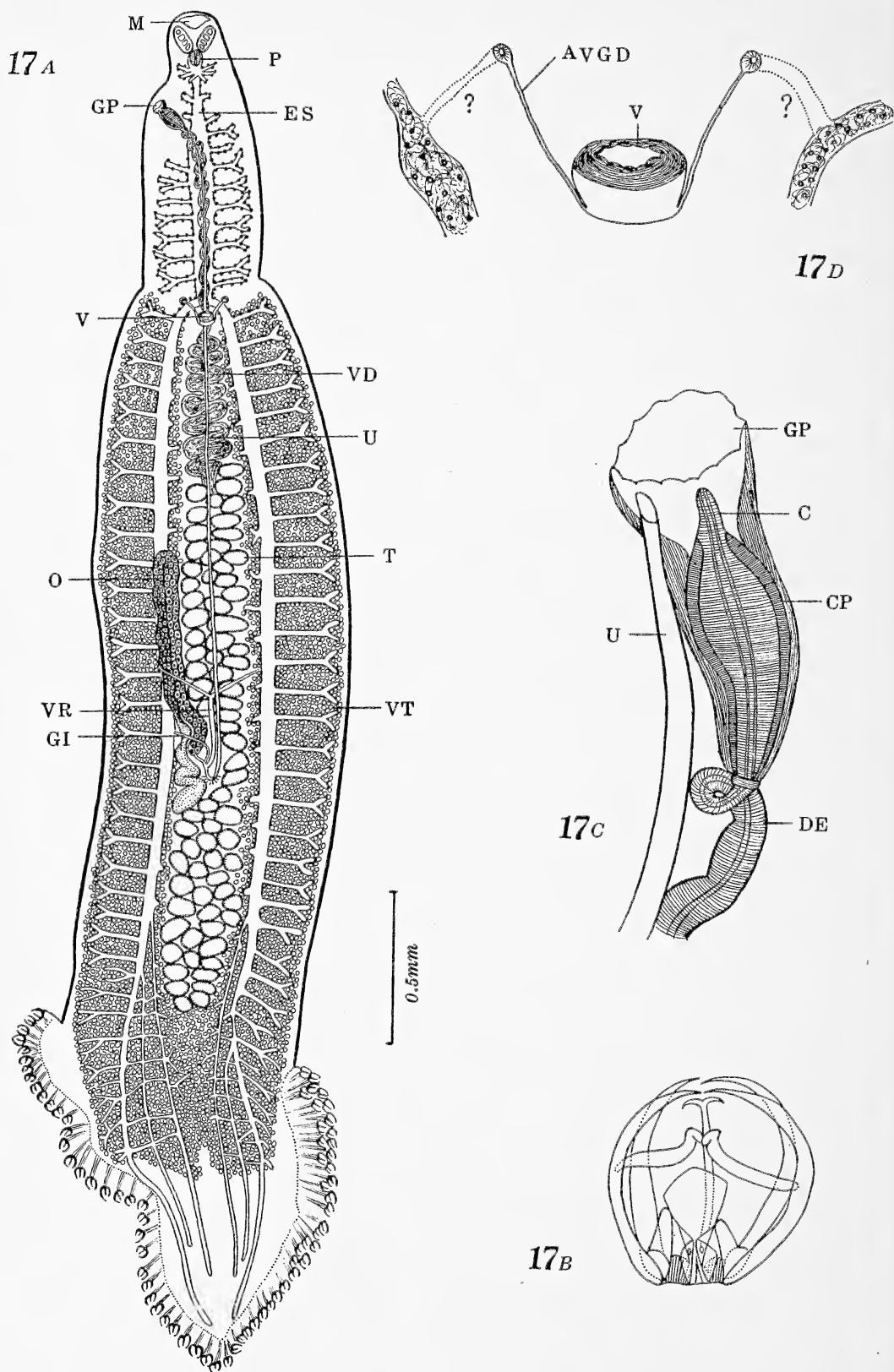
HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 17.

DESCRIPTION (based on 16 whole mounts): Body proper widened from level of anterior end of ovary to cotylophore,  $11-25 \times 4.5-16$  mm, abruptly narrowed anterior to ovary and gradually tapering toward head which is  $0.11-0.21$  mm in diameter. There are 63-105 clamps arranged in an oblique row along entire posterior margin of body proper, whose posterior extremity is prolonged into a conical appendage bearing two pairs of hooks; clamp skeleton consisting of two pairs of arcuate lateral arms, a pair of short basal arms, a pair of accessory sclerites and a median spring; longer prong of median spring anchor-shaped, but shorter prong slightly truncate apically and bearing simple, paired, and a terminally bifid, unpaired, poorly sclerotized, apical pieces just beneath the simple accessory sclerites. Of the caudal hooks the outer pair is  $40-54\mu$  long and the inner pair  $22-30\mu$  long, both with a very prominent guard and a long, well-curved blade. Head end usually rounded, with wide mouth aperture ventrally; at the bottom of the buccal cavity is a pair of comparatively small, aseptate, muscular suckers  $20-33\mu$  by  $27-50\mu$ ; pharynx oval,  $45-60 \times 35-50\mu$ . Esophagus simple,  $0.6-1.6$  mm long, bifurcating a little behind genital pore; intestinal limbs simple anteriorly, sooner or later giving diverticles which unite with one another and form network extending throughout enlarged portion of body proper, enclosing variable number of testes in the meshes.

Testes rounded, separated into 70-170 flat areolae, very irregular in size and outline, commencing at junction of anterior with middle third of body; each areola comprising 1 to 20 testes. Vas deferens strongly twisted posteriorly

when distended with sperm, running in interintestinal field dorsal to uterus but more loosely winding anteriorly and differentiated into a sigmoid pars prostatica surrounded by prostate cells a short distance posterior to genital pore. Ejaculatory duct narrow, winding; cirrus pouch funnel-shaped, containing bulbous cirri at its widest anterior portion, continued into genital atrium; cirrus consisting of a basal bulb  $45-50\mu$  in diameter and an apical bundle of elongate cuticular shingles projecting into genital atrium. The structure and number of the shingles could not be made out, because they are massed tightly together. They appear to arise from the anterior border of the truncate conical, membranous extension of the bulbous cirri. Genital atrium  $65-93\mu$  in diameter, provided with thick wall of circular muscle fibers, provided inside with a crown of 13 to 18 hooks which measure  $40-55\mu$  in length including the cylindrical base  $14-19\mu$  long, each being bifid at the incurved tip. Genital pore ventral to esophagus,  $0.36-0.75$  mm from head end.

Ovary tubular, arising from posterior end of interintestinal field at anterior end of posterior third of body in form of a compact V-shaped mass of very small primordial germ cells, extending forward just medial to left intestinal limb, turning back on itself at about midbody and descending along medial side of ascending portion; as a whole the ovary measures  $2.6-6.5$  mm in length and  $0.12-0.6$  mm in maximum width. The germiduct arising from the distal end of the ovary joins the genito-intestinal duct on the left and then the vitelline reservoir on the right at the posterior end of the middle third of the body. Genito-intestinal duct frequently forming a rounded or elliptical seminal receptacle  $12-25\mu$  in diameter near its origin from germiduct, opening into left intestinal limb, usually at a level a little anterior to its origin. Eggs fusiform, thick-shelled,  $175-265 \times 70-120\mu$  in mounted condition, produced at each end into rigid process which is  $70-200\mu$  long and may or may not terminate in a disc  $8-25\mu$  in diameter. Vagina entirely lacking. Vitellaria completely co-extensive with intestine and its network; their rudimentary follicles commencing along esophagus at varying levels posterior to genital atrium; vitelline reservoir Y-shaped, its stem  $0.45-1.3$  mm long, imme-



diately dextral to distal portion of ovary.

**DISCUSSION:** This obviously gastrocotylid species cannot be assigned to any known genus on account of absence of a vagina and peculiar arrangement of the testes. A new genus and a new subfamily are, therefore, proposed for its reception, referring to the areolate testes.

**Areotestiinae** n. subf.

**SUBFAMILY DIAGNOSIS:** Gastrocotylidae: Clamps unilateral, symmetrical in structure, with accessory sclerites. Hook-bearing caudal appendage present, prehaptor larval anchors absent. Testes divided into numerous groups which are isolated one from another by anastomosing intestinal branches.

**Areotestis** n. g.

**GENERIC DIAGNOSIS:** Gastrocotylidae, Areotestiinae: Haptoral clamps nearly of *Gastrocotyle* type, arranged along straight or arcuate posterior margin of body, the distal end of which is produced into a terminal lappet bearing 2 pairs of anchors. Esophagus simple, long; intestinal limbs with numerous branches anastomosing one another in form of extensive network. Testes divided into numerous areolae of different size and outline and enclosed in meshes of this intestinal network. Pars prostatica distinct, surrounded by prostate cells. Genital atrium muscular, provided inside with a crown of hooks, enclosing armed bulbous cirrus, opening ventral to esophagus. Ovary folded back on itself in posterior interintestinal field, with both ends directed backwards. Genito-intestinal duct short, frequently forming rounded or elongate seminal receptacle. Eggs fusiform, produced into rigid processes at both ends. Vagina absent. Vitellaria co-extensive with intestine and its network, some follicles extending forwards along esophagus; vitelline reservoir in ovarian zone. Gill parasites of marine teleosts.

**TYPE SPECIES:** *A. sibi* n. sp., on gills of *Parathunnus sibi*, *Neothunnus macropterus*, and *Thunnus alalunga*; Hawaii.

18. *Allomicrocotyla onaga* n. g., n. sp.

Fig. 18

**HABITAT:** Gill of *Etelis carbunculus* (local name "onaga"); Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 18.

**DESCRIPTION** (based on five whole mounts): Body proper fusiform to elliptical; opisthohaptor shaped like an asymmetrical fan fringed with two rows of clamps along its semicircular posterior margin which is 0.8–1.4 mm long. At one end of the opisthohaptor there are two pairs of anchors of different size and shape. Total body length 2.5–4.0 mm, maximum width 0.8–1.6 mm in midregion of body proper. Clamps 40–63 in number, arranged in two rows of equal or subequal length, 20–31 in one row and 20–33 in the other; clamp skeleton of uniform structure, consisting of a basally jointed median spring, two pairs of unjointed lateral arms, and a pair of basal sclerites, each of which articulates with the base of the two lateral arms at one end and with the enlarged end of dorsal prong of the median spring at the other end; the narrow solid ventral prong tapers toward its bifid tip reaching the tips of the ventral lateral arms, while the short dorsal prong curves ventrad and terminates in a transversely enlarged solid pad which is united by muscle with another ventrally curved hollow median sclerite reaching to tip of dorsal lateral arms. Head more or less pointed anteriorly, 0.11–0.13 mm wide at level of oral suckers; at the apex is a compact group of gland ducts originating from the group of parapharyngeal, postsuctorial gland cells and passing dorsal to the oral suckers. I prefer to designate the apical group of gland ducts as apical organ, and the parapharyngeal mass of gland cells as apical gland, although the structural details of the gland cell could not be made out except for the granular cytoplasm surrounding the dark-staining nucleus which is definitely larger than the adjoining parenchymatous nuclei. Mouth comparatively wide, opening ventrally at level of base of head. Oral suckers opening into buccal cavity, one on each side of anterior end of pharynx, strongly muscular, aseptate, 40–55 $\mu$  by 50–56 $\mu$ . Pharynx pyriform, 37–65  $\times$  32–51 $\mu$ , cellular except at the apex which is provided with circular muscle fibers. Nerve commissure

FIG. 17. *Pseudocobauhanea sphyraenae* n. g., n. sp. 17A, Holotype, ventral view; 17B, clamp; 17C, terminal genitalia; 17D, vagina and its accessory ducts.

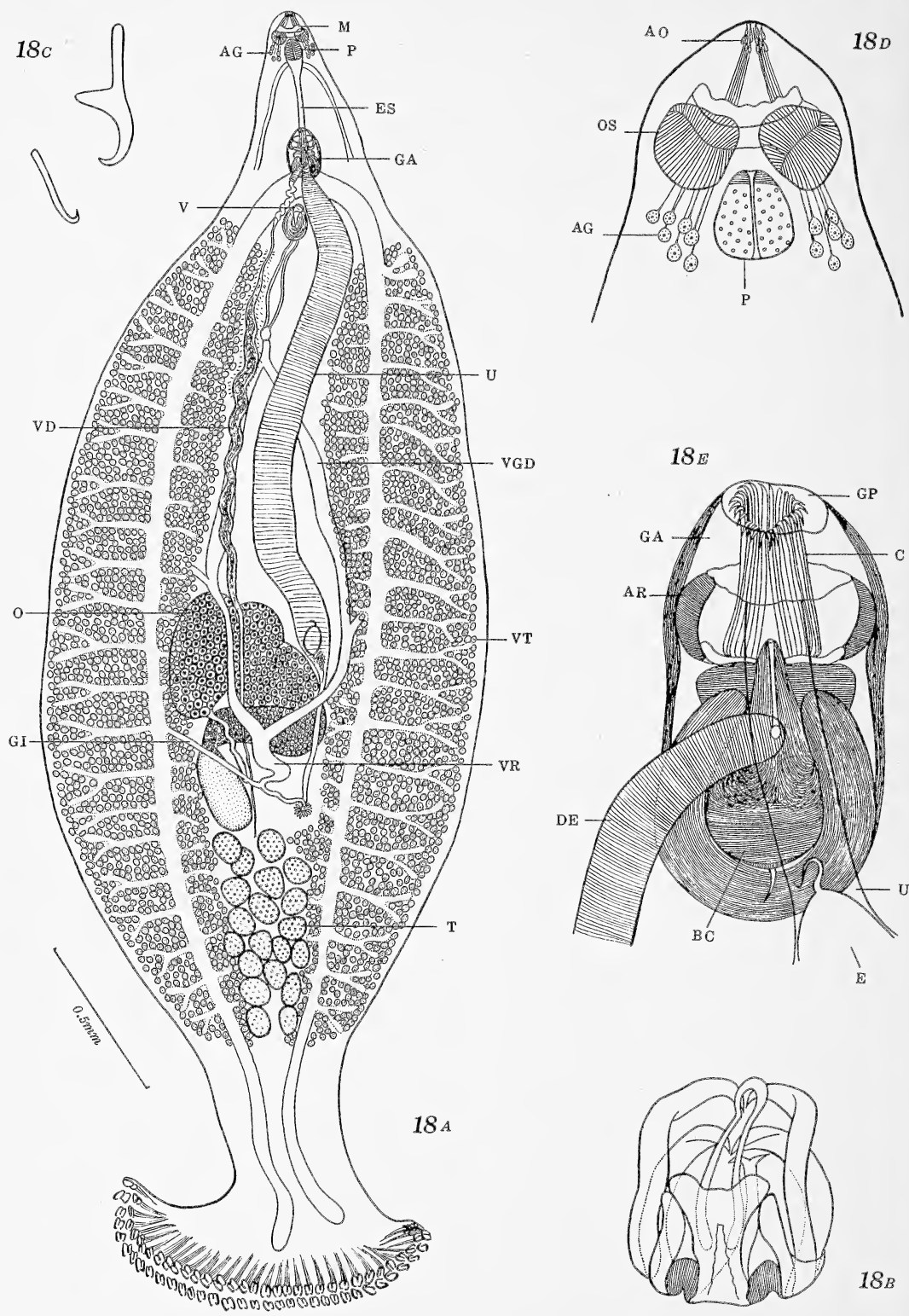


FIG. 18. *Allomicrocotyla onaga* n. g., n. sp. 18A, Holotype, ventral view; 18B, clamp; 18C, caudal anchors; 18D, anterior extremity; 18E, terminal genitalia, ventral view.



and paired nerve trunks conspicuous, former dorsal to anterior end of esophagus. Esophagus simple, without diverticles; intestinal limbs simple at the beginning as well as at the posterior portion intruding into the opisthohaptor, giving off numerous short inner and longer outer branches in swollen region of body proper.

Testes rounded, 10–20 in number, arranged irregularly in postovarian interintestinal field, but not beyond level of posterior end of vitellaria. Vas deferens slightly winding on the right of median line, provided with a dense coat of prostatic cells along greater distal portion. No pars prostatica differentiated. Ductus ejaculatorius wider than distal end of vas deferens, provided with circular muscle fibers. Cirrus complex, consisting of a more or less pointed pyriform bulbus cirri of lamellar muscles enclosed in a horseshoe-shaped pad of lamellar muscles, and an inverted cone, on the anterior base of which is set a midventrally interrupted crown of long, apically outcurved spines projecting into the genital atrium. The pointed conical apex of the bulbus cirri fits into the midventral groove of the above-mentioned cone and projects a little into the base of the genital atrium, whereas the apex of the inverted cone is attached to the mid-dorsal side of the bulbus cirri. The ejaculatory duct leads into the bulbus cirri ventral to this point of attachment. Genital atrium forming a powerful ring ( $69\text{--}84\mu$  in outside diameter) of circular muscle fibers basally, but thin-walled distally, provided with circular and longitudinal muscles; the latter fibers extend backward over the atrial ring and continue to the outer surface of the horseshoe-shaped muscle pad, thus simulating the cirrus pouch. Common genital pore ventral to posterior part of esophagus,  $0.28\text{--}0.35$  mm from head end.

Ovary shaped like an interrogation mark,  $0.5\text{--}0.7 \times 0.35\text{--}0.4$  mm, originating at posterior end of middle third of body to right of median line; its swollen distal portion with three constrictions in the type and occupying whole breadth of interintestinal field; germiduct arising from backwardly directed distal end of ovary, giving off genito-intestinal canal just before joining vitelline duct; ootype immediately anterior to anteriormost testes medial to left intestinal limb.

Genito-intestinal duct crossing proximal portion of ovary and emptying into right intestinal limb. Uterus midventral, very wide, may be distended with numerous eggs, thus occupying greater part of preovarian interintestinal field, opening into genital atrium across anterior rim of atrial ring mentioned above. Uterine eggs elongate oval,  $130\text{--}152 \times 65\text{--}72\mu$ ; anterior filament rather rigid,  $35\text{--}70\mu$  long; posterior filament extremely long and slender, forming close coils at posterior end of egg. Vagina funnel-shaped,  $58\mu$  by  $30\mu$  in the type, provided with circular and longitudinal muscle fibers, opening dorsally just on the right of median line shortly behind intestinal bifurcation; vaginal duct arising from posterior end of vagina, provided with heavily sclerotized walls down to end of its fusiform swelling, then reduced to a narrow duct, but soon becoming enlarged to a small ampulla  $23\text{--}39\mu$  long by  $18\text{--}26\mu$  wide. The comparatively wide duct arising from the posterior end of this ampulla soon ( $70\mu$  behind the ampulla in the type) divides into inverted V-shaped duct distended with yolk cells. Each limb of this duct empties into the lateral arm of the Y-shaped vitelline reservoir of its own side, so that the vagina is directly connected with the vitelline reservoir. Vitellaria co-extensive with intestine and its branches in fusiformly enlarged portion of body proper, leaving simple anterior and posterior portions of intestine free. Vitelline reservoir Y-shaped, largely overlapping ovary.

DISCUSSION: This genus bears a certain resemblance to *Pyragraphorus* Sproston, 1946 and *Allopyragraphorus* Yamaguti, 1963, in general anatomy, but differs fundamentally from either of them in the structure of the clamp skeleton, especially in the paired basal pieces articulating with the median piece. Moreover, the structure of the cirrus is entirely different from that of any of the known members of the Monogenea. In view of these characteristics there is no doubt that the present genus, apparently of microcotyloid type, represents a distinct family.

#### *Allomicrocotyla* n. g.

GENERIC DIAGNOSIS: Microcotyloidea, Allo-microcotylidae: Body proper fusiform; opisthohaptor semicircular, asymmetrical, strongly constricted off from body proper, fringed with

two rows of clamps, with two pairs of anchors of different size and shape at one end. Clamp skeleton quite different from those of *Microcotyle*, *Gastrocotyle*, *Pyragraphorus*, *Allopyragraphorus*, etc. Head with apical organ at front end. Oral suckers strongly muscular, pharynx cellular except for anterior end. Esophagus without diverticles; intestinal limbs simple at beginning and posterior portion intruding into opisthohaptor, branched elsewhere. Testes not very numerous. Cirrus consisting of inverted cone of lamellar muscles inclosed in a horseshoe-shaped pad of lamellar muscles and a crown of stavelike spines set on base of cone; common genital pore ventral to esophagus. Ovary bent back on itself in midregion of body, with its distal end directed backward. Genito-intestinal duct present. Eggs elongated oval, with filament at each pole. Vagina opening dorsally to right of median line shortly behind intestinal bifurcation; vaginal duct connected with paired arms of vitelline reservoir by means of inverted V-shaped duct. Vitellaria largely co-extensive with intestine and its branches; vitelline reservoir Y-shaped, largely overlapping ovary. Gill parasites of marine teleosts.

TYPE SPECIES: *A. onaga* n. sp., on *Etelis carbunculus*; Hawaii.

#### ALLOMICROCOTYLIDAE n. fam.

FAMILY DIAGNOSIS: Microcotyloidea: Opisthohaptor asymmetrical; clamp without apical accessory sclerites; short prong of median spring enlarged at tip and articulated on each side with basal sclerites and also with another dorsal median piece which is stout, hollow and curved ventrad. Anchor-bearing terminal lappet and prehaptoral hooks absent. Testes postovarian; cirrus pouch absent; cirrus armed. Genital atrium unarmed. Vaginal pore nearly middorsal; postbifurcal. Parasites of marine fishes.

TYPE GENUS: *Allomicrocotyla* n. g.

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## Revision of the Genus *Pandanus* Stickman, Part 17 Species, Mostly New, in Borneo, Cambodia, and Vietnam

HAROLD ST. JOHN<sup>1</sup>

IN BORNEO THERE ARE numerous known species of *Pandanus*, while in Cambodia there are but few. Several new ones from those regions are here proposed. Two new ones from Vietnam are also included, as are expanded descriptions and new locality records for certain species of Borneo and of Vietnam.

### SPECIES FROM BORNEO

#### SECTION *Acrostigma*

*Pandanus pumilus* sp. nov. (sect. *Acrostigma*).  
Fig. 206

DIAGNOSIS HOLOTYPE: Licet acaulescens, foliis 63–89 cm longis 7–8 mm latis subcoriaceis supra viridibus licet infra pallidioribus late sulcatis et cum plicis binis rotundatis inermibus, in sectione mediali cum 12–13 nervis secundariis parallelis in quoque latere, nervis tertiis nullis laminis gradatim in apice 15 cm longo trigono subulato diminuentibus eo 10 cm ex apice 3 mm lato, basi amplexicauli inermi purpurea excrassa et valde venosa, ex 4–4.5 cm marginibus cum aculeis 1–1.5 mm longis 1–5 mm separatis subulatis compressis subadscendentibus pallidis, midnervo infra ultra mediam inermi, in sectione mediali marginibus cum serrulis 0.3–0.5 mm longis 2–5 mm separatis adpressis, in apice subulato marginibus et midnervo infra cum serrulis 0.2–0.3 mm longis 0.5–3 mm separatis, ad apicem supra plicis cum serrulis 0.2–0.3 mm longis 4–5 mm separatis, inflorescentia foeminea erecta striata infra nuda parte  $\frac{1}{3}$  infera retrorse scabra, bractea supera 12 cm longo parte  $\frac{1}{4}$  infera 8 mm lata lanceolata foliacea parte  $\frac{3}{4}$  supera trigona subulata, inflorescentia spicata cum 4–5 syncarpiis quaque

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sustenta cum bractea foliosa, ea mediali 2.3 cm longa 1 cm lata lanceolata, ultra mediam marginibus et midnervo infra cum serrulis, syncarpiis 1.5–2 cm longis 1.3–1.5 cm diametro elliptico-subglobozo cum 113–160 drupis, eis 6–7 mm longis 2.5–3.5 mm latis 1.5–3 mm crassis corpore oblanceo-ellipsoideo 5–6 mm longo stramineo valde striato, pileo cum basi 1 mm alto depresso pyramidali 5–6-anguloso luteo et cum vicinis connatis, stylo 1–1.5 mm alto parte basali lanceoloidea apice in angulo recto crasse subulato, stigmati 1–1.5 mm longo distali late lineari nigro papilloso paene in apice extento, endocarpio mediali ellipsoideo 3.8 mm longo cartilagineo stramineo lateribus 0.03 mm crassis, semine 3 mm longo ellipsoideo, mesocarpio apicali minuto, mesocarpio basali 1 mm longo in lateribus fibroso in media carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Apparently acaulescent, or perhaps with short slender stems; leaves 63–89 cm long, 7–8 mm wide, thin coriaceous, green above, apparently slightly paler beneath, broad-furrowed above the midrib and with two rounded pleats, above unarmed, at midsection with 12 or 13 parallel secondary veins in each half, no visible tertiary cross veins, very gradually narrowed to a trigonous subulate apex 15 cm long, this 10 cm down 3 mm wide, the base amplexicaul, unarmed, purple, thin and strongly veiny, beginning 4–4.5 cm from the base the margins with prickles 1–1.5 mm long, 1–5 mm apart, flattened subulate, slightly ascending, pale; the midrib unarmed to beyond the middle; at midsection the margins with appressed serrulations 0.3–0.5 mm long, 2–5 mm apart; on the subulate apex the margins and midrib below with serrulations 0.2–0.3 mm long, 0.5–3 mm apart; towards the apex on the upper side the pleats with serrulations 0.2–0.3 mm long, 4–5 mm apart; pistillate inflorescence erect, striate, naked except

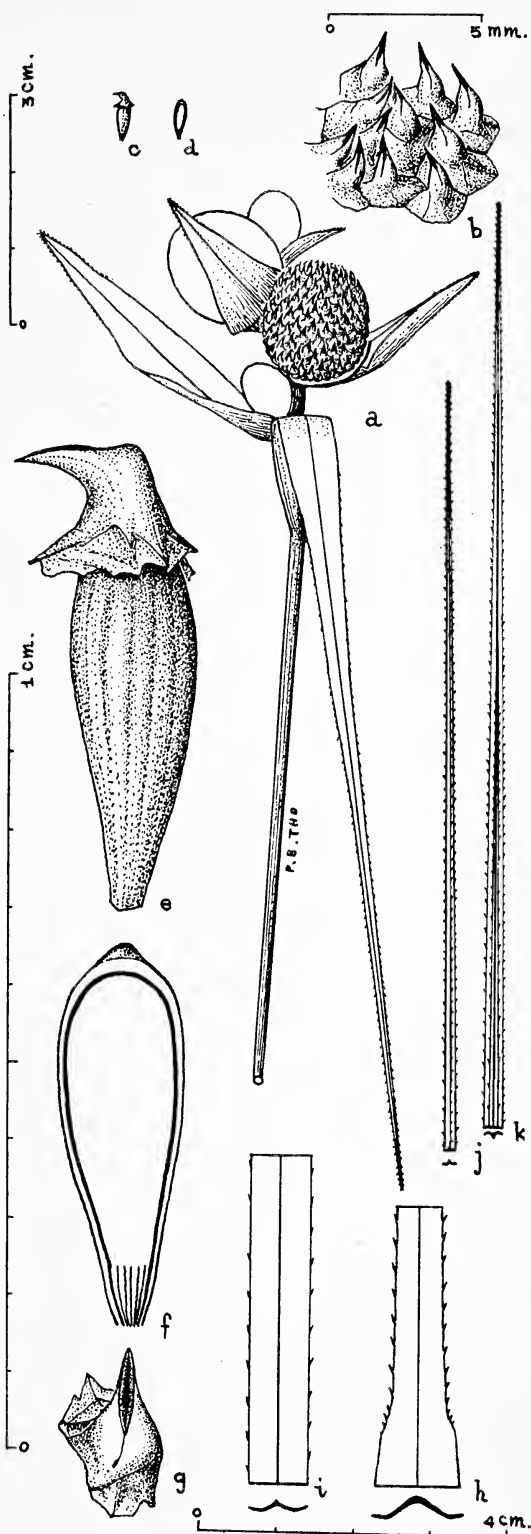
at apex, the lower  $\frac{1}{3}$  retrorse scabrous; apical sterile bract 12 cm long, its lower quarter 8 mm wide, lanceolate, foliaceous, the remainder trigonous subulate; inflorescence spicate, with 4 or 5 syncarps, each subtended by a leafy, apparently green, bract, the median one 2.3 cm long, 1 cm wide, lanceolate, beyond the middle the margins and midrib below serrulate; syncarps 1.5–2 cm long, 1.3–1.5 cm in diameter, elliptic-subglobose, bearing about 113–160 drupes, these 6–7 mm long, 2.5–3.5 mm wide, 1.5–3 mm thick, the body oblance-ellipsoid, 5–6 mm long, stramineous, heavily striate; pileus with the base 1 mm high, low pyramidal, 5–6-angled, at maturity yellow and the adjacent ones connate; style 1–1.5 mm high, this basal portion lanceoloid, bearing proximally at right angles the stout subulate tip; stigma 1–1.5 mm long, distal, broad linear, black, papillose, reaching almost to the tip; endocarp median, ellipsoid, 3.8 mm long, cartilaginous, stramineous, the walls 0.03 mm thick; seed 3 mm long, ellipsoid; apical mesocarp minute; basal mesocarp 1 mm long, fibrous up the walls, fleshy within.

**HOLOTYPUS:** Sarawak, Gunong Pueh, rocks in forest, epiphyte, 3,000 ft. alt., 25 Aug. 1955, J. W. Purseglove 4,799 (SING).

**SPECIMENS EXAMINED:** Sarawak, Nanga Pelagos, Buah Kuning, 24 July 1938, Daud & Tachun 35,645 (SING).

**DISCUSSION:** *Pandanus pumilus* is a member of the section *Acrostigma*, as is its closest relative, *P. fruticosus* St. John of North Borneo, a species which has the syncarp solitary, 3 cm long, 2 cm in diameter, ellipsoid; drupes 9–10 mm long; style arcuate ascending; and the leaves 51–58 cm long, 8–10 mm wide, and the marginal serrations black. *P. pumilus* St. John of Sarawak has the syncarps 4 or 5 in a spike and 1.5–2 cm long, 1.3–1.5 cm in diameter, elliptic-

**FIG. 206.** *Pandanus pumilus* St. John, from holotype. *a*, Infructescence,  $\times 1$ ; *b*, carpel apices and stigmas, oblique distal view,  $\times 4$ ; *c*, drupe, lateral view,  $\times 1$ ; *d*, drupe, longitudinal median section,  $\times 1$ ; *e*, drupe, lateral view,  $\times 10$ ; *f*, drupe, longitudinal median section,  $\times 10$ ; *g*, drupe apex and stigma, apical view,  $\times 10$ ; *h*, leaf base, lower side,  $\times 1$ ; *i*, leaf middle, lower side,  $\times 1$ ; *j*, leaf apex, lower side,  $\times 1$ ; *k*, leaf apex, upper side,  $\times 1$ .



subglobose; drupes 6–7 mm long; style proximally bent at right angles; and the leaves 63–89 cm long, 7–8 mm wide, and the marginal serrations pale.

The new epithet is the Latin adjective *pumilus*, small, and is given in reference to the tiny syncarps and drupes.

#### SECTION *Microstigma*

*Pandanus trigonus* sp. nov. (sect. *Microstigma*)  
Fig. 207

DIAGNOSIS HOLOTYPE: Foliis 2.5 m longis 11 cm latis crassiter coriaceis 1-sulcatis 2-plicatis in sectione mediali cum 55 nervis secundariis parallelis inconspicuis in quoque latere, nervis tertiis obliquis et reticulis breviter rhombicis formantibus, laminis ligulatis longe in apice 35 cm longo subulato trigono diminuentibus eo 10 cm ex apice 3.5 mm lato, proxima basem marginibus cum spinis 2.5–3.5 mm longis 4–10 mm separatis crassiter arcuato-deltoides adscendentibus pallidis, midnervo infra cum spinis 2–3 mm longis 10–20 mm separatis simulantibus infimis reflexis alteris adscendentibus in sectione mediali marginibus cum spinis 2–2.2 mm longis 8–17 mm separatis deltoides compressis salientibus apicibus rubris, midnervo infra cum serris 1.5 mm longis 9–20 mm separatis, in apice subulato marginibus et midnervo infra cum serris 1–1.5 mm longis 6–15 mm separatis crassis, pedunculo foemineo 2 cm diametro trigono, syncarpio licet solitario 26 cm longo 4.5 cm diametro subcylindrico sed parve supra diminuentibus et proxima apicem 3 cm diametro 3-laterato cum circa 1,776 drupis, eis 9–10 mm longis 1.7–2.5 mm latis et crassis distinctis anguste oblanceo-ellipsoideis parte  $\frac{1}{3}$  supera libera, corpore 7–8 mm longo anguste ellipsoideo, pileo 4–5 mm longo laevi dimidia infera oblonga dimidia supera rotundato-pyramidalis apice oblongo-pentagonali truncato, stigmate sessile 0.9–1.3 mm diametro orbiculari vel orbiculari-cordato sessili exelavato brunneo apicem obtecto, endocarpio mediali cartilagineo lateribus brunneis 0.1 mm crassis, semine 5.5 mm longo ellipsoideo, mesocarpio apicali 1.5 mm longo fibroso et medullosa, mesocarpio basali parvo fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Leaf 2.5 m long, 11 cm wide, thick coriaceous, 1-ribbed, 2-pleated, at midsection with 55 parallel secondary veins in each half, these inconspicuous, the tertiary cross veins oblique, forming short rhombic meshes, the blade ligulate, long tapering to a 35 cm subulate, trigonous apex which about 10 cm down is 3.5 mm wide, near the base the margins with spines 2.5–3.5 mm long, 4–10 mm apart, thick arcuate deltoid, ascending, pale, the midrib below with similar spines 2–3 mm long, 10–20 mm apart, the lowest reflexed, the others ascending; at midsection the margins with spines 2–2.2 mm long, 8–17 mm apart, deltoid, flattened, salient, red-tipped; the midrib below with serrations 1.5 mm long, 9–20 mm apart; along the subulate apex the margins and the midrib below with heavy serrae 1–1.5 mm long, 6–15 mm apart; pistillate peduncle 2 cm in diameter, trigonous; syncarp probably single, 20–26 cm long, 4.5 cm in diameter, subcylindric but gently tapering upwards and near the tip 3 cm in diameter, 3-sided, bearing about 1,776 drupes, these distinct, 9–10 mm long, 1.7–2.5 mm wide and thick, narrowly oblance-ellipsoid, upper  $\frac{1}{3}$  free, the body 7–8 mm long, narrowly ellipsoid; pileus 4–5 mm long, smooth, the lower half oblong, the upper half rounded pyramidal to the oblong pentagonal truncate apex; stigma sessile, 0.9–1.3 mm in diameter, orbicular to orbicular-cordate, sessile, flush, brown, covering the apex; endocarp median, cartilaginous, the walls brownish, 0.1 mm thick; seed 5.5 mm long, ellipsoid; apical mesocarp 1.5 mm long, fibrous and pithy; basal mesocarp sparse, fibrous and fleshy.

HOLOTYPE: Sarawak, Bau, H. N. Ridley (SING).

SPECIMENS EXAMINED: British North Borneo, Tawao, Elphinstone Prov., Oct. 1922 to March 1923, A. D. E. Elmer 21,022 (C, M, SING).

DISCUSSION: *P. trigonus* is a member of the section *Microstigma*, as is its closest relative, *P. subumbellatus* Solms of northeast New Guinea, a species with the syncarp 20 cm long, 8–10 cm in diameter, surrounded by long spathes; drupes 12–15 mm long, 3 mm wide; stigmas 1–5 mm wide; and the leaves 6 cm wide. *P. trigonus* St.

John has the syncarp 20–26 cm long, 4.5 cm in diameter; drupes 9–10 mm long, 1.7–2.5 mm wide; stigmas 0.9–1.3 mm wide; and the leaves 11 cm wide.

The new epithet is the Latin adjective *trigonus*, three-angled, and is given in reference to the three-angled syncarp.

#### SECTION *Pandanus*

*Pandanus tectorius* Soland. var. *borneensis* Martelli, Webbia 4(2):410, pl. 19, fig. 6, 1914

Fig. 208

EXPANDED DESCRIPTION: From Wood & Wyatt-Smith A4,567: Shrub, 8.6 m tall; branch apex 3.5 cm in diameter; leaves 84–100 cm long, 4 cm wide, coriaceous, broad furrowed above the midrib, the sides arched and recurving, at midsection with 46 parallel secondary veins in each half, but no visible tertiary veins, blade sword-shaped, tapering gradually to the trigonous, broad subulate apex, this 10 cm down 10 mm wide, the base amplexicaul, unarmed, but beginning 8 cm up the margins with prickles 2–3.5 mm long, 7–13 mm apart, arcuate subulate, ascending, pale; the midrib below beginning at 7–10 cm with prickles 3–3.5 mm long, 17–32 mm apart, heavy subulate, arcuate, reflexed; at midsection the margins with prickles 2–4 mm long, 12–20 mm apart, similar, ascending; the midrib below with prickles 2.5–3.2 mm long, 35–39 mm apart, similar; on the subulate apex the margins with serrulations 0.2–0.3 mm long, 2–4 mm apart; the midrib below with similar serrulations but 3–6 mm apart; phalanges 5.3–5.8 cm long, 2.9–3.5 cm wide, 2.5–2.9 cm thick, pyriform, 4–5-angled, the sides gently convex, smooth, shining, when dried light brown, upper ½ free, the apex convex, lateral sutures none, central apical sinuses 1–2 mm deep, very shallow but the bottom half V-shaped; carpels 6 or 7, the apices low obtuse and the marginal ones with a small concavity distal of the stigma, the outer carpels 1½–2 times the larger; stigma 3–3.5 mm long, elliptic, creased, dark brown, elevated; proximal sinus a wide crack running ⅓–½ way to valley bottom; endocarp slightly supramedian, 22 mm long, bony, the inner parts dark mahogany

colored, the outer parts pale, the lateral walls 4–5 mm thick, the inner surfaces shining; seeds 14–16 mm long, 3–4 mm in diameter, ellipsoid or obliquely so; upper mesocarp forming in each carpel apex a cavity with brownish medullary membranes; basal mesocarp fibrous and fleshy.

SPECIMENS EXAMINED: North Borneo, Sipitang District, Sibubu River, Mengalong Forest Reserve, 5 miles s. w. of Sipitang, 5 ft. alt., 30 July 1954, G. H. S. Wood & J. Wyatt-Smith A4,567 (SING).

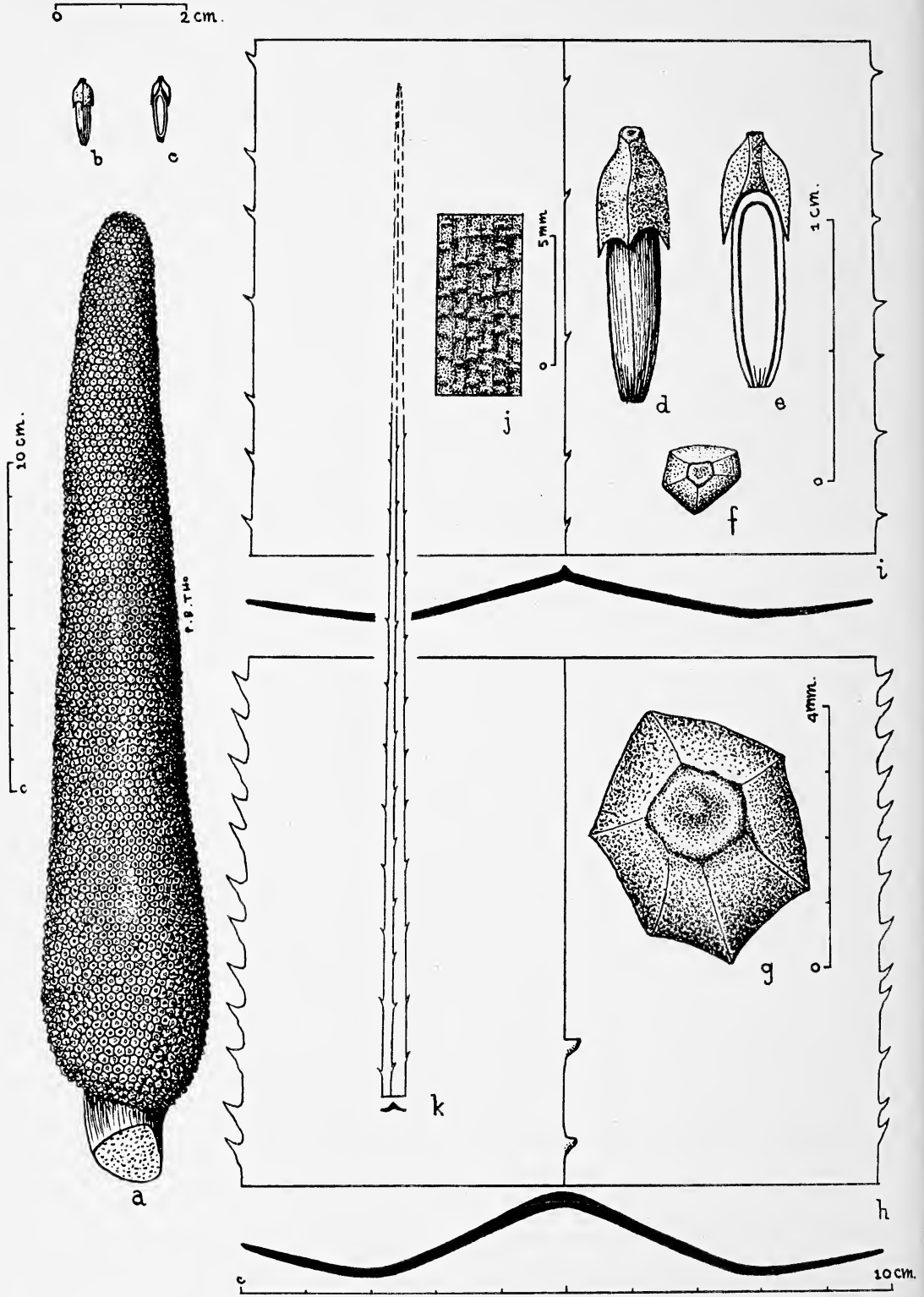
#### SPECIES FROM CAMBODIA

#### SECTION *Acrostigma*

*Pandanus pendens* sp. nov. (sect. *Acrostigma*)  
Figs. 209, 213a, b

NOM. VERN.: "rhom cheak."

DIAGNOSIS HOLOTYPE: Frutex 7–8 m alta 4 cm diametro erecta multi-ramosa, cortice brunneo et cum spinis 7–10 mm longis anguste conicis, radicibus futurosis 20–40 cm longis 1 cm diametro spinosis paucis, foliis 85–92 cm longis 2.8–3 cm latis supra obscure viridibus infra pallidis et glaucis ligulatis coriaceis in sectione mediali cum 28 nervis secundariis in quoque dimidio gradatim ex basi in apice subulato diminuentibus eo 10 cm ex apice 3 mm lato, basi amplexicauli et inermi sed ex 4.5–5 cm marginibus cum dentibus 1.5–2 mm longis 3–8 mm separatis subulato-serratis, midnervo infra ad mediam inermi, in sectione mediali marginibus cum serris 0.7–1 mm longis 4–6 mm separatis adpressis, proxima apicem marginibus et midnervo infra cum serrulis 0.2–0.3 mm longis 2–4 mm separatis, pedunculo 20–35 cm longo 10–12 mm diametro obtuse trigono folioso-bracteato sed bracteis deciduis, syncarpio solitario terminali pendenti 7–10 cm longo 6–8 cm diametro latiter ellipsoideo, drupis numerosissimis 27–32 mm longis 2.5–3 mm latis 1.5–2 mm crassis sublinearibus 4–6-angulosis parte ¼ supra libera, pileo laevi anguste ovoideo-conico sed aliquis obliquis et proxime inclinatis deciduis, stylo 2.5–3 mm longo subulato proxime arcuato cartilagineo, stigmatem 2–2.5 mm longo distali sublineari brunneo exlaevi, endocarpio in parte ⅔ infera cartilagineo brunneo lateribus 0.1 mm crassis, semine 6–7 mm longo ellipsoi-



deo, mesocarpio apicali viridi mucilaginoso sed in sicco cavernoso et 12 mm longo, mesocarpio basali in lateribus fibroso sed intra carnosio.

DIAGNOSIS OF HOLOTYPE: Shrub, 7–8 m tall, 4 cm in diameter, erect, freely branched above; bark brown, with sharp, narrow, conic spines 7–10 mm long; prop roots few, 20–40 cm long, 1 cm in diameter, spiny; leaves 85–92 cm long, 2.8–3 cm wide, dark green above, pale and glaucous below, ligulate, coriaceous, at midsection with 28 parallel secondary veins in each half, gradually tapering from the base to the subulate apex, this 10 cm down 3 mm wide, the very base cuneate widened, amplexicaul, unarmed, but beginning 4.5–5 cm up the margins with teeth 1.5–2 mm long, 3–8 mm apart, subulate-serrate; midrib unarmed as far as the middle; at midsection the margins with appressed serrae 0.7–1 mm long, 4–6 mm apart; near the tip the margins and the midrib below with serrations 0.2–0.3 mm long, 2–4 mm apart; peduncles 20–35 cm long, 10–12 mm in diameter, obtusely trigonous, leafy bracted but the bracts deciduous before the fruit matures; syncarp single, terminal, pendent, said to become “20 cm. long and yellow,” but those seen nearly mature (with well-formed seeds) 7–10 cm long, 6–8 cm in diameter, broad ellipsoid; drupes very numerous, 27–32 mm long, 2.5–3 mm wide, 1.5–2 mm thick, almost linear, 4–6-angled, upper  $\frac{1}{4}$  free; pileus smooth, narrowly ovoid-conic, but somewhat oblique and inclined proximally, deciduous; style 2.5–3 mm long, subulate, proximally arcuate, cartilaginous; stigma distal, 2–2.5 mm long, almost linear, brown, rough; endocarp in lower  $\frac{2}{3}$ , cartilaginous, brown, the walls 0.1 mm thick; seed 6–7 mm long, ellipsoid; apical mesocarp continuous, green, mucilaginous but on drying shrinking to form a cavity 12 mm long; basal mesocarp fibrous along periphery, fleshy within.

HOLOTYPE: Cambodia, 1 km. s. of Ph. Khdat,  $\frac{1}{2}$  km. inland, 16 km. w. of Kampot, in narrow, wooded stream gulch some 10 m. deep,

15 m. alt., May 19, 1960, *Harold St. John* 26,344 (BISH).

DISCUSSION: *P. pendens* is a member of the section *Acrostigma*, as is its closest relative, *P. pectinatus* Martelli of Sarawak, a species with the drupes 27 mm long, 3–4 mm wide, linear oblong; endocarp in lower  $\frac{1}{5}$ , enclosing a conic cavity half as long and just above the seed cavity. *P. pendens* St. John of Cambodia has the drupes 27–32 mm long, 2.5–3 mm wide, cuneate; endocarp in lower  $\frac{2}{3}$ , not enclosing a superior cavity.

Local inhabitants reported that the leaves are used for plaiting mats, and that after drying they are boiled to make a medicine for fevers of children.

The new epithet is the Latin participle *pendens*, hanging, given in reference to the posture of the fruit.

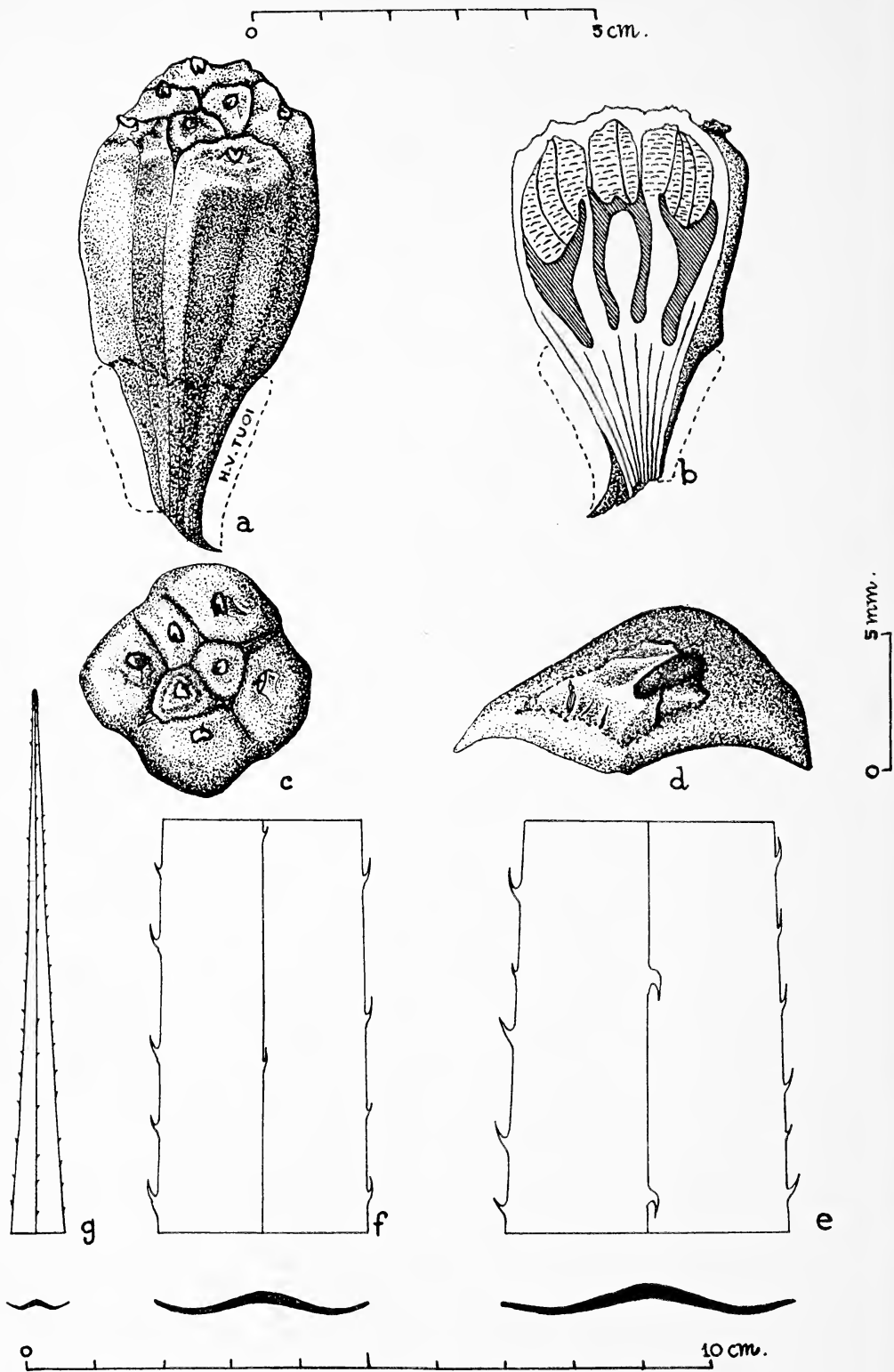
SECTION *Rykia*

*Pandanus cupribasalis* sp. nov. (sect. *Rykia*)  
Figs. 210, 213c, d

NOM. VERN.: “rhom cheak.”

DIAGNOSIS HOLOTYPE: Frutex 2–4 m alta 3–5 cm diametro cum ramis erectis pluribus plerumque simplicibus, cortice brunneo laevi vel cum radicillis spinosis paucis, radicibus futuriosis 30–60 cm longis 1 cm diametro sublaevibus sed cum radicillis conicis paucis remotis, foliis multis 1.48 m longis 3.8–4 cm latis supra obscure viridibus infra viridibus late sulcatis et subplicatis ligulatis sed in 20 cm ultimis in apice trigono subulato abrupte diminuentibus eo in puncto 10 cm ex apice 1.6 mm lato, in sectione mediali cum 31–34 nervis secundariis parallelis in quoque latere et ad apicem infra cum nervis tertiis transversis evidentis et reticulis anguste oblongis formantibus, basi amplexicauli inermi intense cupracea et ex 15–25 cm marginibus cum spinis 4–5 mm longis 12–18 mm separatis crassiter subulatis arcuatis adscendentibus pallidis excepta apicibus

FIG. 207. *Pandanus trigonus* St. John, from holotype. a, Syncarp,  $\times 1$ ; b, drupe, lateral view,  $\times 1$ ; c, drupe, longitudinal median section,  $\times 1$ ; d, drupe, lateral view,  $\times 4$ ; e, drupe, longitudinal median section,  $\times 4$ ; f, drupe, apical view,  $\times 4$ ; g, drupe, apical view,  $\times 10$ ; h, leaf base, lower side,  $\times 1$ ; i, leaf middle, lower side,  $\times 1$ ; j, secondary and tertiary veins, lower side, at middle,  $\times 4$ ; k, leaf apex, lower side,  $\times 1$ .





brunneis, midnervo infra ex 25 cm cum aculeis 5–7 mm longis 18–22 mm separatis crassiter subulatis reflexis, in sectione mediali marginibus cum aculeis 1.8–2 mm longis 10–25 mm separatis subulatis adpressis adscendentibus, midnervo infra subinermi, proxima apicem marginibus et midnervo infra cum serrulis 0.3–0.6 mm longis 2–6 mm separatis, pedunculo 50 cm longo in apice 13 mm diametro infra graciliori folioso-braceato cernuo terminali, syncarpio unico 16.5 cm longo 8 cm diametro oblongo-ellipsoideo 3-laterato cum circa 540 drupis et superficie spinoso ex stylis salientibus, drupis 25–30 mm longis 7–10 mm latis 5–9 mm crassis cuneato-oblancoeloideis viridibus sed apparente lutescentibus laevibus 6-lateratis lateribus planis parte  $\frac{1}{4}$  supera libera, pileo pyramidali-semiorbiculari, stylo 3–4 mm longo valido osseoso crasso lucido corniformi brunneo in  $40^\circ$  adscendenti latiter bifido (rare trifido, et eis apicalibus simplicibus), stigmatibus 3 mm longo plerumque latiter ovato et in apice bifido brunneo papilloso, endocarpio minime submediali aurantiaco-brunneo lateribus 2 mm crassis, semine 8–9 mm longo 3 mm diametro anguste ellipsoideo; mesocarpio apicali cavernoso et cum fibris longitudinalibus paucis et membranis medullosis, mesocarpio basali fibroso et carnoso.

**DESCRIPTION OF ALL SPECIMENS EXAMINED:** Shrub 2–4 m tall, 3–5 cm in diameter, with several erect, mostly simple stems; bark brown, smooth, or with a few latent rootlets; prop roots few, 30–60 cm long, 1 cm in diameter, smooth, except for a few remote conic rootlets; leaves in terminal plumes, numerous, 1.48–3.6 m long, 3.8–4 cm wide, above dark green, below green, with a broad central groove and gently down curved outer quarters, ligulate, then about 20 cm from the tip abruptly narrowed into a subulate trigonous tip which 10 cm down is 1.6 mm wide, at midsection with 31–34 parallel secondary veins in each half, towards the apex the lower side with evident tertiary cross veins making a reticulum of narrow oblong meshes, the amplexicaul, hidden base unarmed, bright

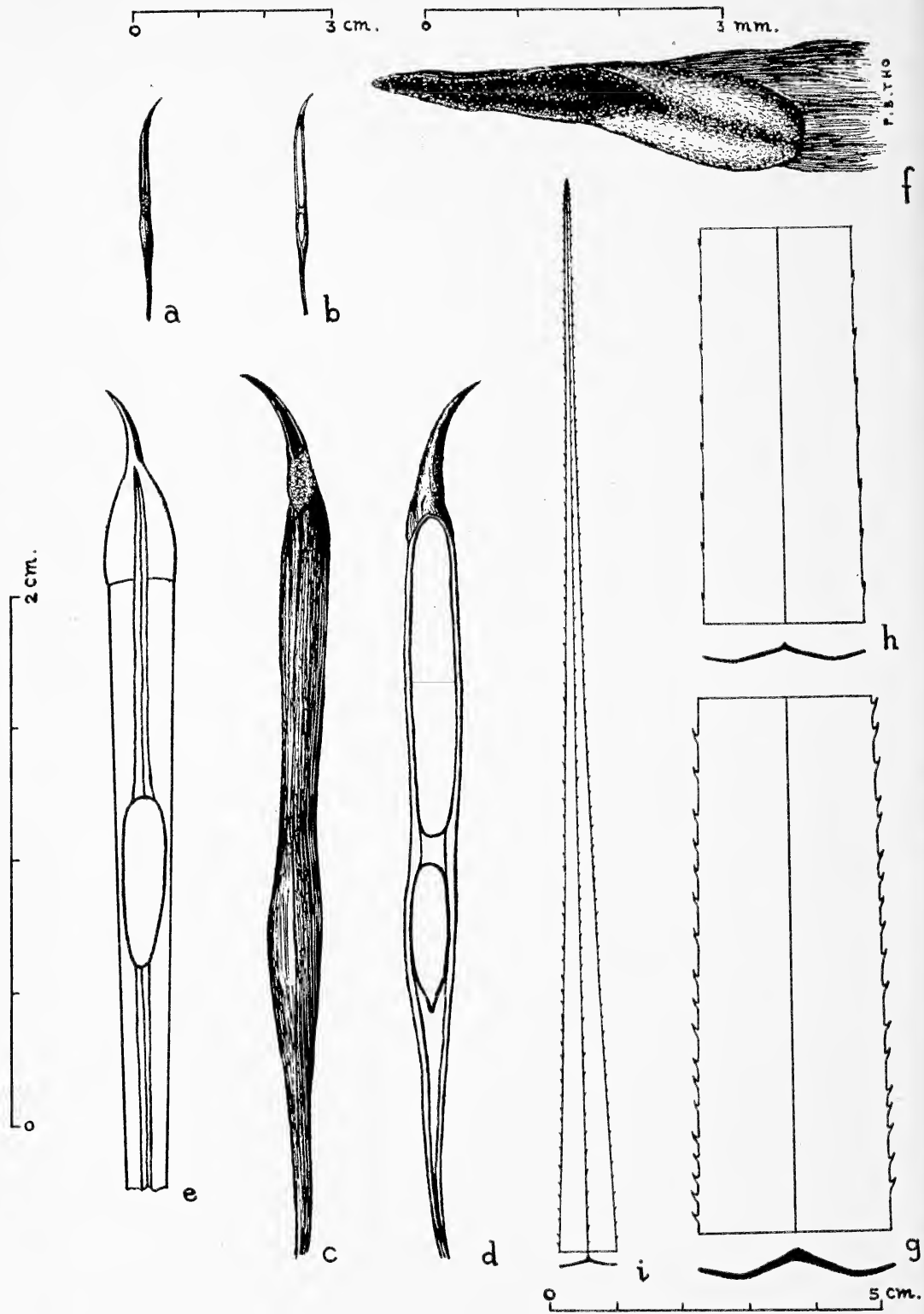
copper-orange, beginning at 15–25 cm up the margins with spines 4–5 mm long, 12–18 mm apart, heavy subulate, arcuate, ascending, pale, but the tip brownish; the midrib below, beginning 15–25 cm from the base with stout subulate spines 5–7 mm long, 18–22 mm apart, reflexed; at midsection the margins with prickles 1.8–2 mm long, 10–25 mm apart, subulate, appressed ascending, the nearby midrib below almost unarmed; near the apex the margins and midrib below with serrulations 0.3–0.6 mm long, 2–6 mm apart; peduncle 50 cm long, at apex 13 mm in diameter, tapering and more slender downwards, leafy bracted, nodding, terminal; syncarp single, 16.5 cm long, 8 cm in diameter, oblong-ellipsoid, distinctly 3-sided, with about 540 drupes, the surface thorny from the projecting styles; drupes 25–30 mm long, 7–10 mm wide, 5–9 mm thick, cuneate-oblancoeloid, still green, apparently becoming yellowish, the surface smooth, 6-sided, the sides plane, upper  $\frac{1}{4}$  free; pileus pyramidal-semiorbicular; stylar beak 3–4 mm long, stout, bony, shining, brownish, ascending at about  $40^\circ$ , almost all widely bifid, but rarely one is trifid, and the apical ones 1-dentate; stigma 3 mm long, mostly broad ovate and bifid at apex, brown, papillose; endocarp slightly submedian, orange-brown, the lateral walls 2 mm thick; seed cavity 8–9 mm long, 3 mm in diameter, narrowly ellipsoid, traversed by longitudinal fibers; apical mesocarp cavernous, with a few longitudinal fibers and medullary membranes; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Cambodia, Chaine de l'Elephant, on the mountain grade 12 km. below Le Bokor, dense moist fern forest, with *Ficus*, *Homalanthus*, and *Hicriopteris*, 1,000 m. alt., May 20, 1960, *H. St. John* 26,346 (BISH).

**SPECIMENS EXAMINED:** Cambodia, Bokor, common in ever green forest, 900 m. alt., 21 Feb. 1960, *Tem Smitinand* 6,534 (BKF).

**DISCUSSION:** *P. cupribasalis* is a member of the section *Rykia*, as is its closest relative, *P. furcatellus* Martelli, of Indochina, a species with

FIG. 208. *Pandanus tectorius* Soland. ex Warb. var. *borneensis* Martelli, from Wood & Wyatt-Smith A4,567. a, Phalange, lateral view,  $\times 1$ ; b, phalange, longitudinal median section,  $\times 1$ ; c, phalange, apical view,  $\times 1$ ; d, carpel apex and stigma, oblique view,  $\times 4$ ; e, leaf base, lower side,  $\times 1$ ; f, leaf middle, lower side,  $\times 1$ ; g, leaf apex, lower side,  $\times 1$ .



the syncarp covered with bracts, solitary, erect; styles ovate, acute; endocarp 1.5 cm long, the lateral walls 0.8 mm thick; seed cavity truncate at apex, 6 mm in diameter; leaves 8 cm wide, near the base the margins with spines 6 mm long, 14–23 mm apart, stout arcuate subulate, the tips brownish, on the midrib below the spines 7–8 mm long, 22–40 mm apart, similar but reflexed and the tips slender. *P. cupribasalis* has the syncarp exposed, solitary, nodding; styles lanceolate, acute; endocarp 2 cm long, the lateral walls 2 mm thick; seed cavity ellipsoid, 4 mm in diameter; leaves 3.8–4 cm wide, near the base the margins with spines 4–5 mm long, 12–18 mm apart, those of the nearby midrib below 5–7 mm long, gradually narrowed to a long subulate apex.

The new epithet is formed from the Latin *cuprum*, copper; *basalis*, of the base, and is given in allusion to the strikingly copper-colored leaf bases.

#### SPECIES FROM VIETNAM

##### SECTION *Rykia*

*Pandanus depressus* sp. nov. (sect. *Rykia*)

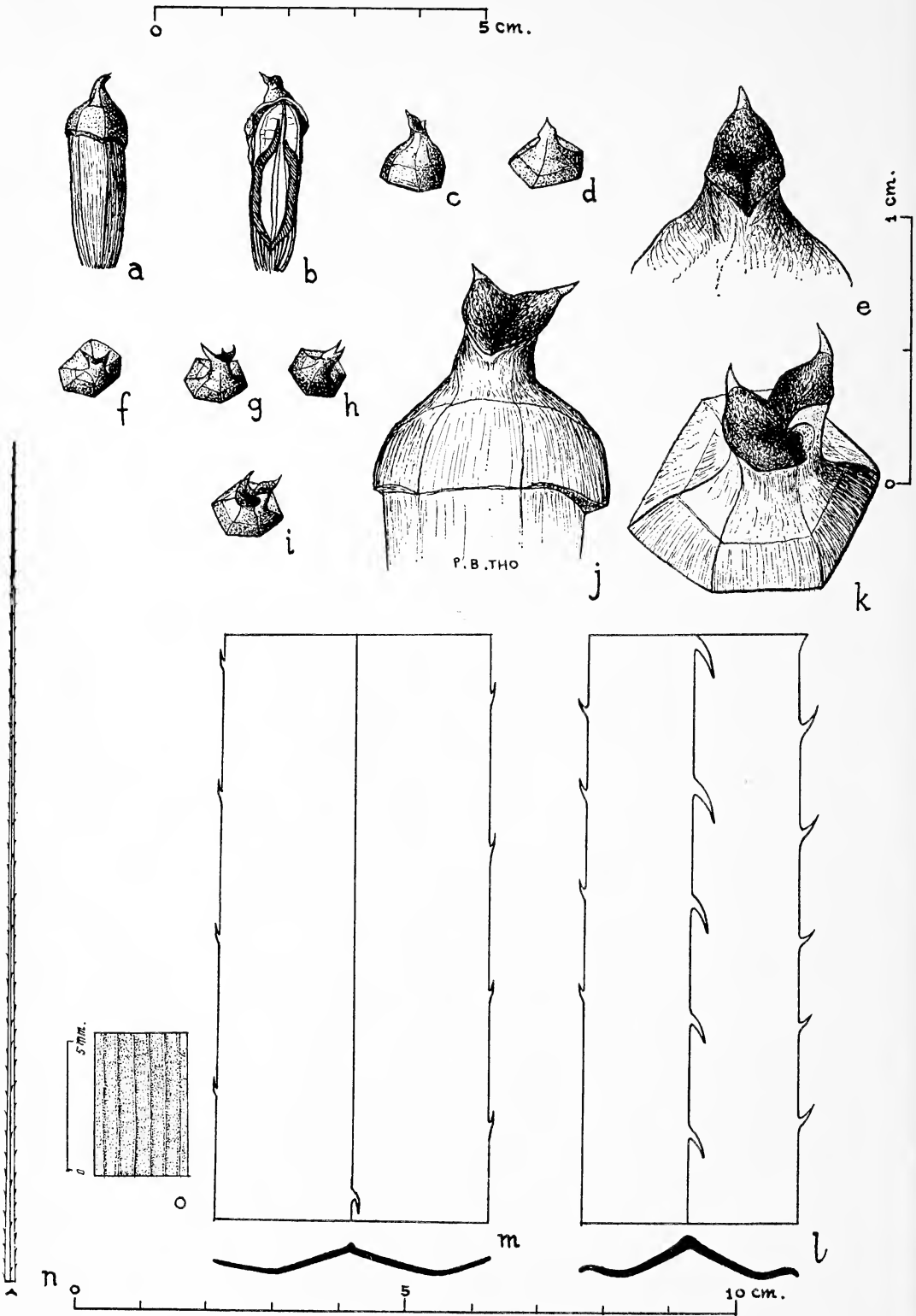
Figs. 211, 214a

DIAGNOSIS HOLOTYPE: Caulibus folisque non conservatis (collector dicet ad *P. horizontalis* simulantibus, id est caule 1.5 m alto 4–5 cm diametro cum radicillis adpresse adscendentibus paucis, foliis 2.72 m longis 3.8 cm latis olivaceis 2-plicatis ligulatis abrupte in apice subulato caudato contractis, marginibus et midnervo infra cum aculeis validis), inflorescentia foeminea terminali cum syncarpio solitario, pedunculo 17 cm vel ultra longo 12 mm diametro 3-laterato folioso-bracteato, syncarpio 15 cm longo 8 cm diametro cylindrico cum apicibus rotundatis et cum circa 816 drupis submaturis viridibus, drupis in lineis subverticalibus eis basalibus et apicalibus minime latioribus, drupis 30–32 mm longis 8–12 mm latis 6–10 mm crassis anguste cuneatis 6-angulosis parte  $\frac{1}{6}$  supera libera cor-

pore 26–28 mm longo, pileo cum basi 5–6 mm alto valde depresso rotundato-pyramidali laevi glauco, stylo terminali validi corniformi subrecto vel minime proxime curvato eis apicalibus valde curvato 1.5–2 mm alto furcis 2–3 mm longis horizontali-divergentibus osseosis acutis paucis cum lobis lateralibus binis proximalibus, stigmatibus 1.5–2.5 mm longis lanceolatis brunneis papillosis non ad apices extentis semiproximalibus et terminalibus, endocarpio submediali osseoso brunneo et cum apice mediali acuminato lateribus 1 mm crassis, semine 8–9 mm longo 4 mm diametro obovoideo, mesocarpio apicali meduloso molli albo exfibroso, mesocarpio basali in lateribus fibroso in centro carnoso.

DIAGNOSIS OF HOLOTYPE: Stem and leaves not collected (but said by the collector to be similar to his no. 2,519, *P. horizontalis*; that is, stem 1.5 m tall, 4–5 cm in diameter, with a few appressed ascending rootlets; leaves 2.72 m long, 3.8 cm wide, olive green, 2-pleated, ligulate, abruptly contracted to a caudate, subulate apex, the margins and midrib below with stout prickles); pistillate inflorescence terminal, bearing one syncarp; peduncle more than 17 cm long, 12 mm in diameter, 3-sided, leafy bracted; syncarp 15 cm long, 8 cm in diameter, cylindric with rounded ends, bearing about 816 drupes, somewhat immature, green, but with hard endocarp and well-formed seeds, probably nearly full size; drupes arranged in nearly vertical rows, the basal and apical drupes slightly broader, but not significantly so; drupes 30–32 mm long, 8–12 mm wide, 6–10 mm thick, narrowly wedge-shaped, 6-angled, upper  $\frac{1}{6}$  free, the body 26–28 mm long; pileus with its base 5–6 mm high, much depressed, rounded pyramidal, smooth, glaucous; style terminal, stout, hornlike, suberect or slightly curved proximally, the apical ones definitely so, 1.5–2 mm high, the two forks lanceolate, 2–3 mm long, spreading horizontally, hard, sharp, mucronate and unpleasant to handle, sometimes with 2 small proximal lateral lobes; stigmas 1.5–2.5 mm long, lanceolate, brown, papillose, not reaching to the tip, semiproximal

FIG. 209. *Pandanus pendens* St. John, from holotype. *a*, Drupe, lateral view,  $\times 1$ ; *b*, drupe, longitudinal median section,  $\times 1$ ; *c*, drupe, lateral view,  $\times 4$ ; *d*, *e*, drupe, longitudinal median section,  $\times 4$ ; *f*, carpel apex and stigma, distal view,  $\times 15$ ; *g*, leaf base, lower side,  $\times 1$ ; *h*, leaf middle, lower side,  $\times 1$ ; *i*, leaf apex, lower side,  $\times 1$ .



and terminal; endocarp submedian, bony, brown, with an apical subulate prolongation, the walls 1 mm thick; seed 8–9 mm long, 4 mm in diameter, obovoid; apical mesocarp soft white, pithy, without fibers; basal mesocarp fibrous up the periphery, fleshy within.

**HOLOTYPE:** Vietnam, Hon Tho'm, île S. de Phu qu'ôc, bord de ruisseau, 30–50 m. de rivage, à l'ombre des arbres, 7 janvier 1961, *Pham Hoang Ho 2,530* (BISH).

**DISCUSSION:** *P. depressus* is a member of the section *Rykia*, as is its closest relative, *P. horizontalis* St. John, a species from the same island, but with syncarp broadly ellipsoid, 10.5 cm long; terminal and subterminal drupes the larger; pileus base conic; styles often with 2–4 secondary lobes; stigmas terminal; endocarp in lower  $\frac{1}{3}$ , the walls 0.1 mm thick; seed 2.5 mm in diameter. *P. depressus* has the syncarp cylindric, 15 cm long; drupes all about the same size; pileus base much depressed rounded pyramidal; styles sometimes with 2 secondary lobes; stigmas semiproximal and terminal; endocarp submedian, the walls 1 mm thick; and the seed 4 mm in diameter.

The new epithet is the Latin adjective *depressus*, depressed, and is given in reference to the depressed rounded pyramidal pileus base.

*Pandanus horizontalis* sp. nov. (sect. *Rykia*)

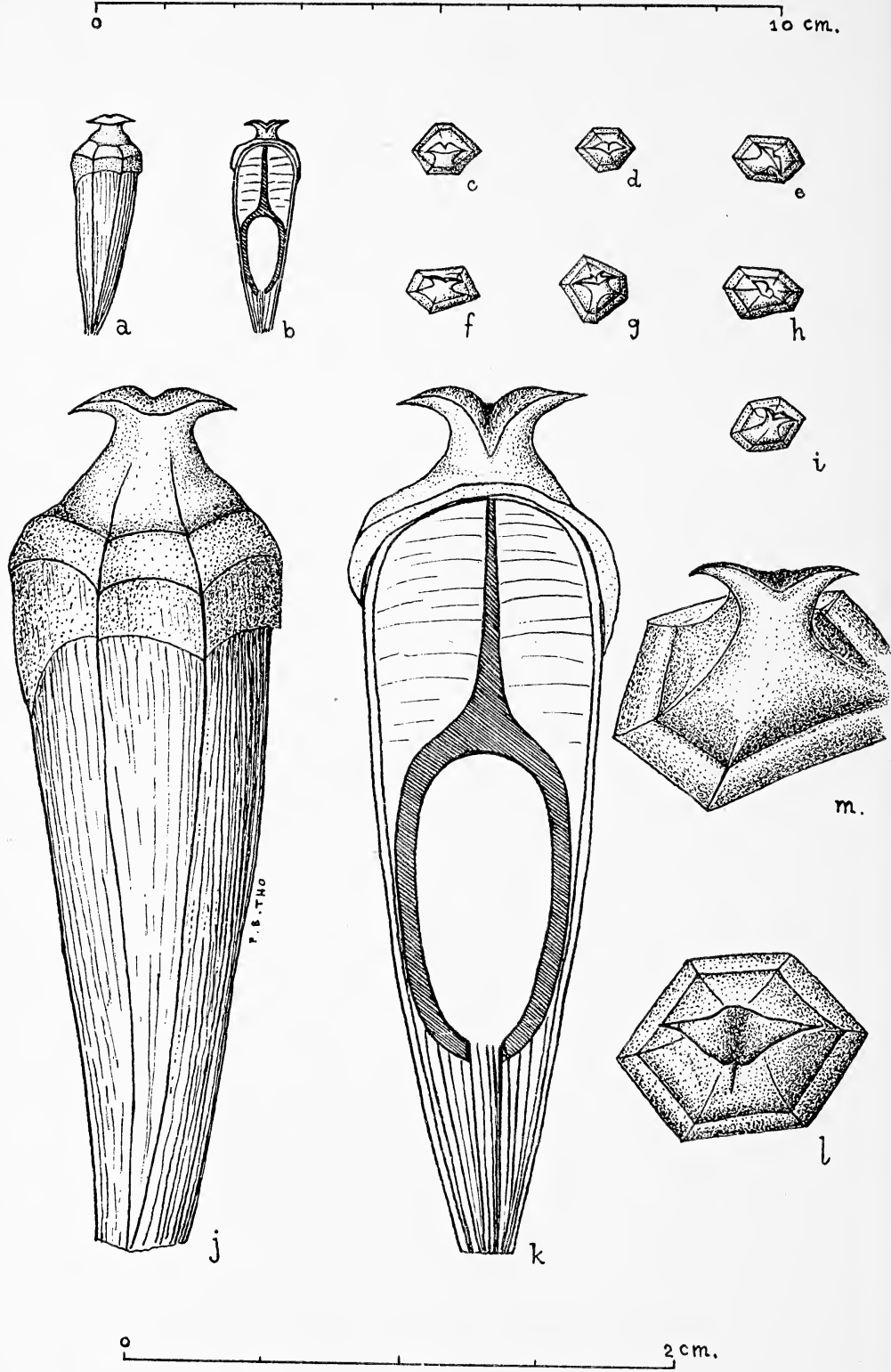
Figs. 212, 214b

**DIAGNOSIS HOLOTYPE:** Caulibus 1.5 m altis 4–5 cm diametro lucidis cum radicillis adpresse adscendentibus paucis, foliis 2.72 m longis 3.8 cm latis infra olivaceis supra obscure ita et profunde sulcatis 2-plicatis, in sectione mediali cum 33 nervis secundariis parallelis in quoque latere, proxima apicem nervis tertiis transversis evidentis et reticulis oblongis formantibus, lamina ligulata in apice 20 cm longo trigono subulato caudato abrupte contracta eo 10 cm ex apice 1 mm lato, basi amplexicauli inermi exlucida cupacea et ex 10–14 cm marginibus cum aculeis

2–4 mm longis 9–18 mm separatis crassiter subulatis rectis adscendentibus apicibus brunneis, midnervo infra ex 8 cm cum spinis 3–4 mm longis 17–35 mm separatis conicis reflexis brunneis, in sectione mediali marginibus cum aculeis 2–3 mm longis 15–25 mm separatis crassiter subulatis adpresse adscendentibus albis sed apicibus brunneis, midnervo infra cum spinis reflexis eis basalibus simulantibus sed 6–8 cm separatis, in sectione apicali diminuenti marginibus et midnervo infra cum serris 0.5–1 mm longis 1.5–5 mm separatis, in apice subulato marginibus cum serrulis 0.3–0.5 mm longis 1.5–3 mm separatis translucentis sed apicibus brunneis, inflorescentia foeminea terminali cernua cum syncarpio unico, pedunculo 45 cm longo 1.8 cm diametro 3-laterato folioso-bracteato, bracteis interioribus 15 cm longis 4.4 cm latis lanceolatis marginibus et midnervo infra serratis, syncarpio 10.5 cm longo, 7.8 cm diametro latiter ellipsoideo cum circa 720 drupis, eis submaturis viridibus lutescentibus eis lateralibus 26–27 mm longis 6–9 mm latis 5–7 mm crassis anguste oblanceoloideis parte  $\frac{1}{6}$  supra libera illis terminalibus et subterminalibus 30–31 mm longis 9–11 mm latis 7–10 mm crassis anguste oblanceoloideis 6-angulosis corpore 25–28 mm longo, pileo cum basi 5–6 mm alta rotundato-conica 6-angulosa laevi viridi subglauca, stylo druparum lateralium erecto solido bifurcato furcis lanceolatis acerosis in angulis rectis divergentibus, stigmatibus lanceolatis brunneis papillosis terminalibus sed lobatis in stylis multis cum lobulis secundariis, basi 1–2 mm longa lobis principalibus 2.5–3.5 mm longis, endocarpio in parte  $\frac{1}{3}$  infera brunneo ellipsoideo acuminato lateribus 0.1 mm crassis cartilagineis, semine 12 mm longo 2.5 mm diametro ellipsoideo, mesocarpio apicali medullosa humido sine fibris, mesocarpio basali 3 mm longo in lateribus fibrosis in centro carnosio.

**DIAGNOSIS OF HOLOTYPE:** Stem 1.5 m tall, 4–5 cm in diameter, shining, with a few appressed ascending rootlets; leaves 2.72 m long,

FIG. 210. *Pandanus cupribasalis* St. John, from holotype. *a*, Drupe, lateral view,  $\times 1$ ; *b*, drupe, longitudinal median section,  $\times 1$ ; *c*, *d*, *f*, *b*, *i*, typical lateral drupes, apical view,  $\times 1$ ; *e*, apex and stigma of apical drupe, proximal view,  $\times 4$ ; *j*, apex and stigma of typical lateral drupe, proximal view,  $\times 4$ ; *k*, apex and stigma of rare 3-fid lateral drupe, apical view,  $\times 4$ ; *l*, leaf base, lower side,  $\times 1$ ; *m*, leaf middle, lower side,  $\times 1$ ; *n*, leaf apex, lower side,  $\times 1$ ; *o*, veins, lower side, towards apex,  $\times 4$ .



3.8 cm wide nearly throughout, olive green below, darkly so above with a deep furrow over the midrib, 2-pleated, at midsection with 33 secondary parallel veins in each side, and near the tip tertiary cross veins visible, forming oblong meshes; blade ligulate, abruptly contracted to a 20 cm subulate, trigonous, caudate apex, this 10 cm down 1 mm wide, the base amplexicaul, unarmed, dull coppery, beginning at 10–14 cm the margins with prickles 2–4 mm long, 9–18 mm apart, heavy subulate, straight, ascending, brown-tipped; the midrib below beginning at 8 cm with thorns 3–4 mm long, 17–35 mm apart, conical, reflexed, brown; at midsection the margins with prickles 2–3 mm long, 15–25 mm apart, thick subulate, appressed ascending, white below, with a brown tip; the midrib below with reflexed spines like the basal ones but 6–8 cm apart; where the blade narrows the margins and midrib below with serrations 0.5–1 mm long, 1.5–5 mm apart; on the subulate apex the margins with serrulations 0.3–0.5 mm long, 1.5–3 mm apart, brown-tipped, but the rest clear and translucent; pistillate inflorescence terminal, cernuous, with a single syncarp; peduncle 45 cm long, 1.8 cm in diameter, 3-sided, leafy bracted; the inner bracts 15 cm long, 4.4 cm wide, lanceolate, serrate on margins and midrib below; syncarp 10.5 cm long, 7.8 cm in diameter, broadly ellipsoid, bearing about 720 drupes, these immature, green, but some turning yellowish, the lateral ones 26–27 mm long, 6–9 mm wide, 5–7 mm thick, narrowly oblanceoloid, upper  $\frac{1}{3}$  free, the terminal and subterminal ones 30–31 mm long, 9–11 mm wide, 7–10 mm thick, narrowly oblanceoloid, 6-angled, the body 25–28 mm long; pileus with its base 5–6 mm high, rounded conic, 6-angled, smooth, green, slightly glaucous; style of lateral drupes erect, stout, bifurcate, the forks lanceolate, spreading horizontally, acrose tipped; stigmas lanceolate, brown, papillose, terminal, but on the many styles with 2–4 short proximal secondary lobes, running over them also, style base 1–2 mm

long, main lobes 2.5–3.5 long; endocarp in lower  $\frac{1}{3}$ , brown, ellipsoid, with an apical subulate extension to the style, the walls cartilaginous, 0.1 mm thick; seed 12 mm long, 2.5 mm in diameter, ellipsoid; apical mesocarp a moist pith, without fibers; basal mesocarp 3 mm long, fibrous up the periphery, fleshy within.

**HOLOTYPE:** Vietnam, île Hon Tho'm, s. of Ile Phu qu'óc, 7 avril 1961, *Pham Hoang Ho 2,519* (BISH).

**DISCUSSION:** *P. horizontalis* is a member of the section *Rykia*. It has the hornlike, bifurcate style of that section and on the terminal and subterminal drupes the style is bent proximally and the stigmas are proximal as is normal. On all the lateral drupes, which are very numerous, the style is erect, with its forks extending laterally at right angles, and the stigmas are terminal. This is exceptional, but from the fact that the style is hornlike, and bifurcate, and that some of them incline in the proximal direction, it is concluded that this new species really belongs in the section *Rykia*.

No close relative of this new species has been described. The closest is an undescribed species from Thailand, Chanturi, *Tem Smitinand 4,054*, but this has smaller, broader drupes, etc.

The new epithet is the Latin adjective *horizontalis*, horizontal, and is given in reference to the horizontal forks of the style and the stigmas.

#### LOCALITY RECORDS OF PANDANUS IN VIETNAM

##### *Pandanus ceratostigma* Martelli

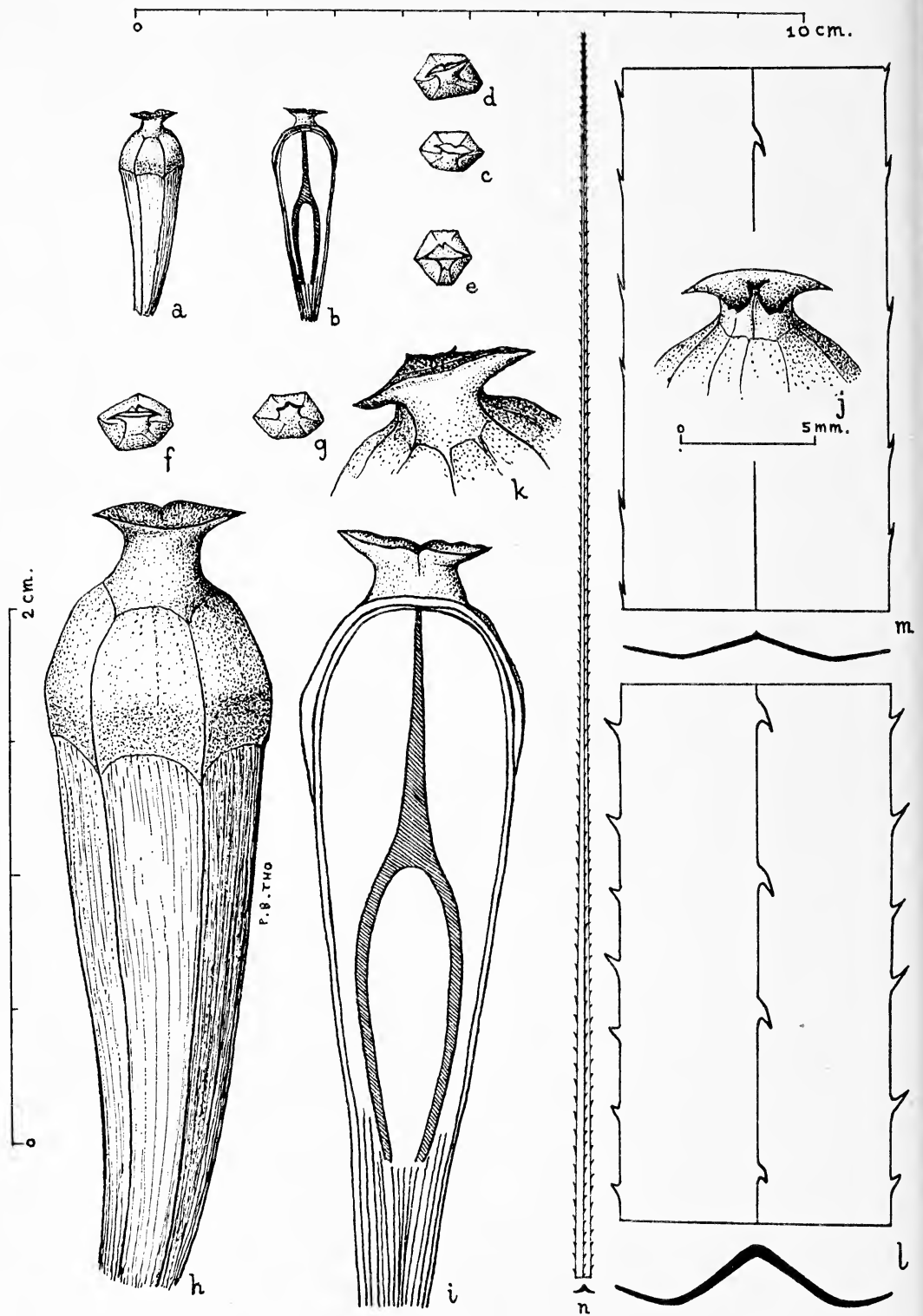
Region de Long câu, Col de Tuy lu'at, at km. 1,267, male, 6 fevrier 1961, *P. H. Ho 2,605* (BISH, UNIV. SAIGON). Also his no. 2,610.

Col de Dio Cà (Varella), près du poste militaire, km. 1,364, 6 fevrier 1961, *Pham Hoang Ho 2,604* (BISH, UNIV. SAIGON).

##### *Pandanus integriapicis* St. John

Prov. de Phu yên, Anthan (Tuyan), km.

FIG. 211. *Pandanus depressus* St. John, from holotype. *a*, Drupe, lateral view,  $\times 1$ ; *b*, drupe, longitudinal median section,  $\times 1$ ; *c*, *d*, *e*, *f*, *g*, *h*, *i*, drupe, apical view,  $\times 1$ ; *j*, drupe, lateral view,  $\times 4$ ; *k*, drupe, longitudinal median section,  $\times 4$ ; *l*, drupe apex and stigma, apical view,  $\times 4$ ; *m*, drupe apex and stigma, oblique distal view,  $\times 4$ .







a



b



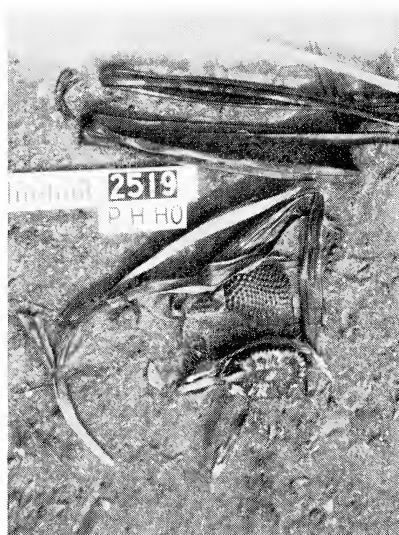
c



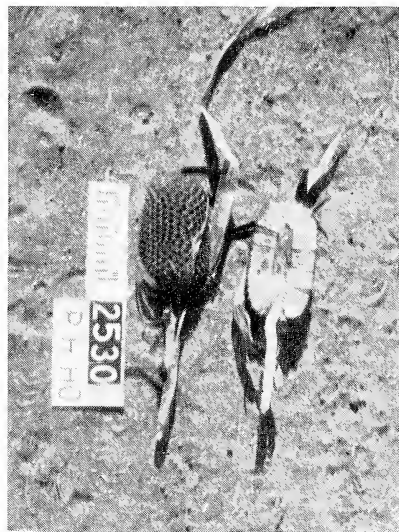
d

FIG. 213. a, *Pandanus pendens* St. John, holotype, habit; b, fruiting branch; c, *Pandanus cupribasalis* St. John, holotype, fruiting stalk; d, branch with syncarp.

FIG. 212. *Pandanus horizontalis* St. John, from holotype. a, Drupe, lateral view,  $\times 1$ ; b, drupe, longitudinal median section,  $\times 1$ ; c, d, e, f, g, drupe, apical view,  $\times 1$ ; h, drupe, lateral view,  $\times 4$ ; i, drupe, longitudinal median section,  $\times 4$ ; j, drupe apex and stigma, proximal view,  $\times 4$ ; k, drupe apex and stigma, distal view,  $\times 4$ ; l, leaf base, lower side,  $\times 1$ ; m, leaf middle, lower side,  $\times 1$ ; n, leaf apex, lower side,  $\times 1$ .



a



b

FIG. 214. *a*, *Pandanus depressus* St. John, holotype, syncarp, lateral view, and longitudinal median section; *b*, *Pandanus horizontalis* St. John, holotype, leaf and syncarp, lateral view, and longitudinal median section.

1,291, 6 février 1961, *Pham Hoang Ho* 2,608 (BISH, UNIV. SAIGON).

*Pandanus Smitinandii* St. John

Prov. de Phu yên, Anthanh (Tuyen), km. 1,291, les haies, les bourgeons donnés aux cochons, 6 février 1961, *Pham Hoang Ho* 1,291 (UNIV. SAIGON); km. 1,260, cultivé au bord du cours d'eau et en bordure du rivièrè, 6 février

1961, *Pham Hoang Ho* 2,609 (BISH, UNIV. SAIGON).

*Pandanus vietnamensis* St. John

Nhatrang, 1.5 km. du gare, près du chemin de fer, à bifurcation pour aller à Ninhhoa, cultivé, 6 février 1961, *Pham Hoang Ho* 2,611 (BISH, UNIV. SAIGON).

# Revision of the Genus *Pandanus* Stickman, Part 18 *Pandanus* of Christmas Island, Indian Ocean, and of the Anamba Islands, Indonesia

HAROLD ST. JOHN<sup>1</sup>

FROM CHRISTMAS ISLAND in the Indian Ocean H. N. Ridley described two species of *Pandanus*. As these were never illustrated, they are given a revised treatment here. Previously Martelli had described a species from the same island, based solely upon fragmentary staminate material. The material of these species in the herbarium at Singapore has been studied anew and is here reported upon.

In the same herbarium is good material of a *Pandanus* from the Anamba Islands, at the northwest border of Indonesia.

## SECTION *Pandanus*

*Pandanus elatus* Ridl. (sect. *Pandanus*), R. Asiat. Soc., Straits Br., Jour. 45:239-240, 1906  
Figs. 215, 216

DIAGNOSIS OF LECTOTYPE: Tree; trunks few and together, 13.3-20 m tall, 15 cm in diameter; bark gray and sparingly thorny; prop roots few, hard, short; leaves 1.77-2.1 m long, 8-10 cm wide, coriaceous, furrowed above the midrib, 2-plicate, in section M-shaped, at midsection with 50-52 parallel secondary veins in each half, tertiary cross veins visible below in outer third forming short oblongs or rhombics, blade ligulate, tapering into a trigonous, subulate apex about 10 cm long, this about 5 cm down 1 mm wide, the base not seen, near the base the margins with spines 2-4 mm long, 4-7 mm apart, the first conical and divergent, the others subulate, ascending from a conic base, the tips red-brown; the midrib below near the base with spines 3 mm long, 11-22 mm apart, with a heavy conic base and a subulate reflexed tip; at midsection the margins with prickles 3-3.5 mm long, 4-10 mm apart, arcuate subulate, flattened;

the midrib below with prickles 2.5-3 mm long, 10-25 mm apart, broad subulate, flat, arcuate ascending; on the subulate apex the margins and midrib below with subulate serrulations 0.3-0.6 mm long, 1-3 mm apart; peduncle "2 feet long and 2½ inches thick"; syncarp solitary, 30-33 cm long, 17.5 cm in diameter, "oblong"; phalanges 7.5-7.7 cm long, 4.5-5.5 cm wide, 3.1-4 cm thick, cuneate-obovoid in profile, 6-7-angled, the side gently curving, smooth, shining, when dried brown, upper ⅓ free, the apex convex, lateral sutures mostly distinct, narrow and deep, central apical sinuses 5-20 mm deep; carpels 9-12, the apices lance-pyramidal, the outer ones more or less diverging, the inner erect and ½-¼ the size of the outer; stigmas 3-3.5 mm long, cordate, sharply oblique and centripetal, creased, brown, flush; proximal sinus usually running to the valley bottom; endocarp submedian, 35 mm long, bony, blackish brown, the lateral walls 3 mm thick, the inner surfaces shining; seeds 18-20 mm long, 5-6 mm in diameter, oblique ellipsoid; upper mesocarp cavernous in each carpel apex, with pale pith and a few fibers; basal mesocarp fibrous and fleshy.

STAMINATE PLANT: Leaves 1.78 m long, 5.5 cm wide, at midsection with 35 parallel secondary veins in each half, tertiary veins obscure, near the base the margins with prickles 1.5 mm long, 4-9 mm apart, stout arcuate subulate, ascending, brown-tipped; the midrib below with prickles 13-18 mm apart, heavy based but the tips broken off; at midsection the margins with prickles 1-1.5 mm long, 3-5 mm apart, stout subulate, flattened, arcuate ascending; the midrib below with prickles 1 mm long, 18-32 mm apart, arcuate, conic, ascending; on the subulate apex the margins and midrib below with subulate serrations 0.2-0.3 mm long, 1-2 mm apart; staminate inflorescence 45 cm long; peduncle fleshy; bracts colored, softer than the leaves; lowest floral bract 40 cm long, 4 cm wide, lance-

<sup>1</sup> B. P. Bishop Museum, Honolulu 17, Hawaii, U.S.A. Manuscript received October 17, 1961.

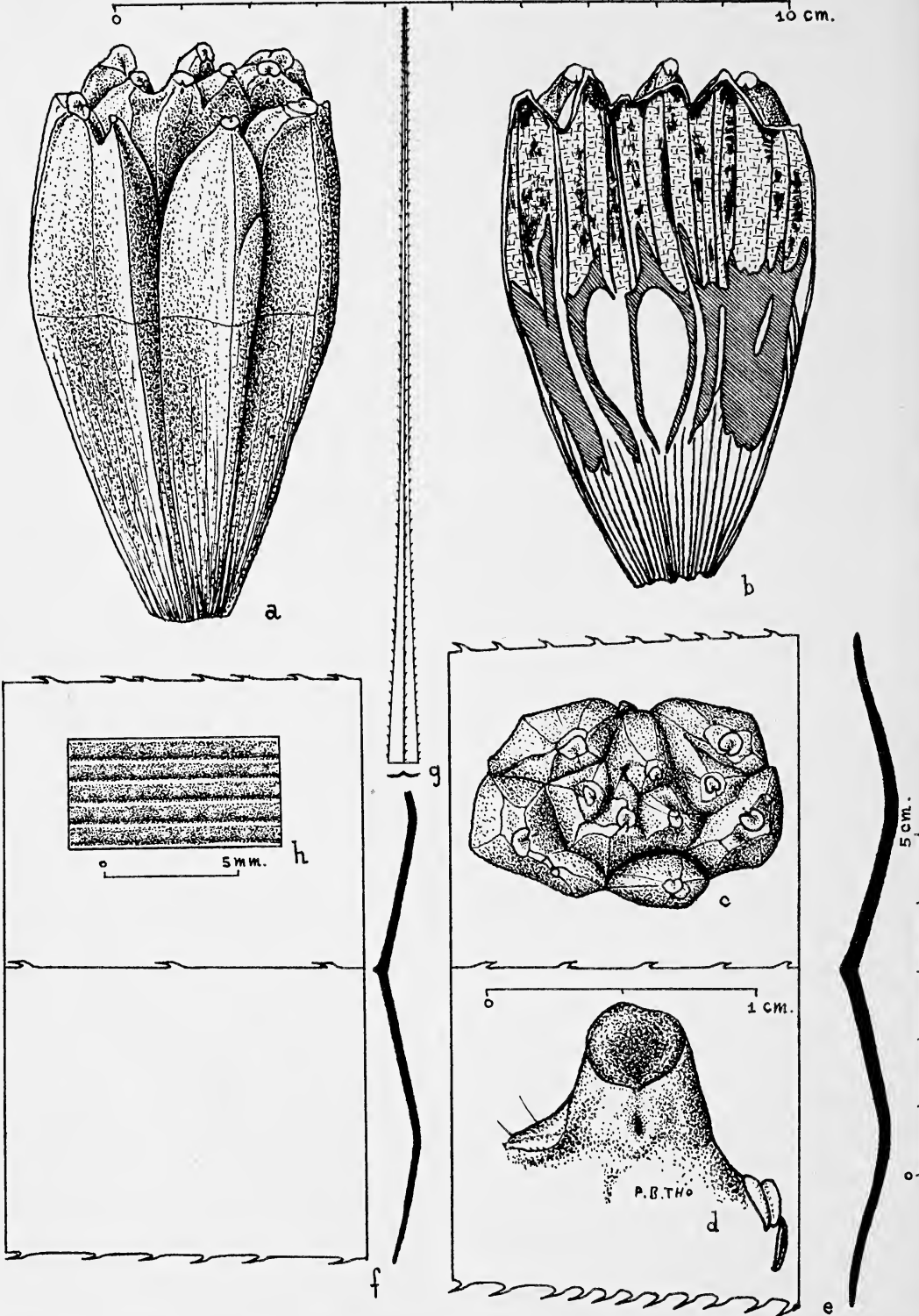


FIG. 215. *Pandanus elatus* Ridl., from holotype. *a*, Phalange, lateral view,  $\times 1$ ; *b*, phalange, longitudinal median section,  $\times 1$ ; *c*, phalange, apical view,  $\times 1$ ; *d*, carpel apex, stigma, and proximal sinus, oblique view,  $\times 4$ ; *e*, leaf base, lower side,  $\times 1$ ; *f*, leaf middle, lower side,  $\times 1$ ; *g*, leaf apex, lower side,  $\times 1$ ; *h*, leaf veins at middle, lower side,  $\times 4$ .

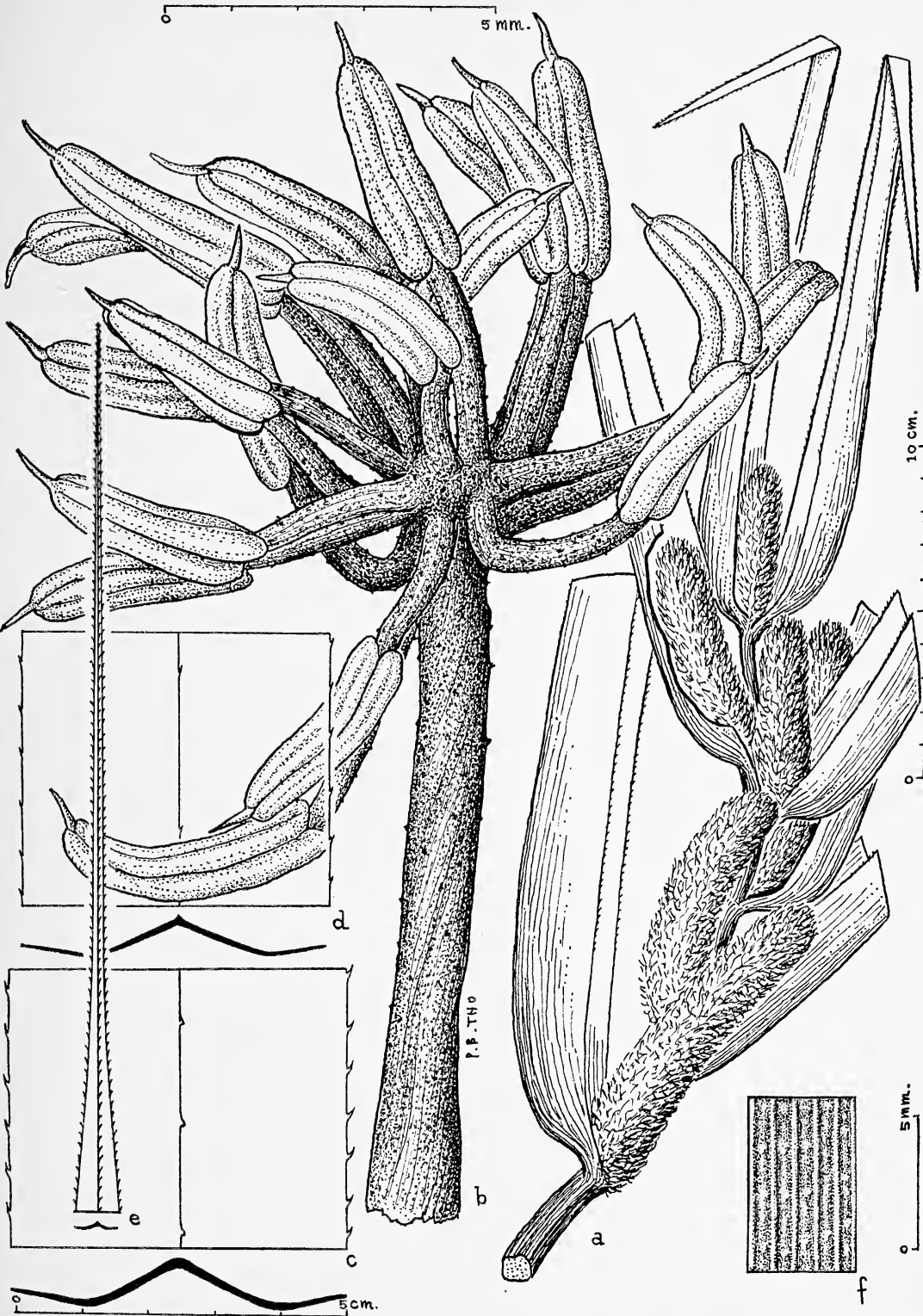


FIG. 216. *Pandanus elatus* Ridl., from Murray Hill Track, H. N. Ridley. *a*, Staminate inflorescence,  $\times \frac{1}{2}$ ; *b*, column, filament tips, and anthers,  $\times 10$ ; *c*, leaf base, lower side,  $\times 1$ ; *d*, leaf middle, lower side,  $\times 1$ ; *e*, leaf apex, lower side,  $\times 1$ ; *f*, leaf veins at middle, lower side,  $\times 4$ .

ligulate, the margins with salient prickles 1–1.5 mm long, 1–2 mm apart; spikes about 7–10 and 6–9 cm long, 1.5–2 cm in diameter, densely flowered; stamens in fascicles 12–18 mm long, with 15–23 anthers; column 7–9 mm long, papillose, bearing the anthers at its apex in an umbel; free filament tips 2–5 mm long, minutely papillose; anthers 3–4 mm long, more or less narrow oblong, but tapering upwards, bearing at its tip a 0.4–0.6 mm subulate projection of the connective.

LECTOTYPE: Indian Ocean, Christmas Island, plateau, Oct. 1904, *H. N. Ridley* (SING). Type examined! Isotype (K)!

SPECIMENS EXAMINED: Christmas Island, Murray Hill Track, Oct. 1904, (staminate), *H. N. Ridley* (SING).

*Pandanus nativitatis* Ridl. (sect. *Pandanus*),  
R. Asiat. Soc., Straits Br., Jour. 45:238–  
239, 1906  
Fig. 217

DIAGNOSIS OF HOLOTYPE: "Bushy; branches about 2.7–4.7 m. tall; leaves 2 m. or more long," 6.4 cm wide, coriaceous, at midsection with 46 or 47 secondary parallel veins in each half, but no visible tertiary cross veins, swordlike, gradually tapering to the 12 cm trigonous subulate apex, this 10 cm down 4 mm wide, lamina furrowed above the midrib and with 2 rounded pleats, the base not preserved, but near it the margins with prickles 1–3 mm long, 2–5 mm apart, stout subulate, pale, somewhat ascending; the midrib below, beginning at about 27 cm with prickles 2–2.5 mm long, 10–24 mm apart, slender subulate, arcuate, ascending; at midsection the margins with prickles 1–1.5 mm long, 3–6 mm apart, subulate, appressed ascending; the midrib below with prickles 1–1.5 mm long, 6–11 mm apart, deltoid subulate, slightly ascending; the subulate apex with the margins essentially unarmed; the midrib below with serrulations 0.3–0.4 mm long, 2–5 mm apart; pistillate inflorescences terminal, bearing one syncarp; peduncle more than 12 cm long, 2 cm in diameter, 3-sided, leafy bracted; syncarp "orange, as big as a man's head." Phalanges (3 seen) 5.3–5.7 cm long, 5 cm wide, 4.3 cm thick, cuneate quadrate, the apex low convex, upper  $\frac{2}{3}$  free, lateral sutures deep in free part, the

sides flattish or gently convex, smooth, shining, 5-angled; sinuses of small central apices 2 mm deep, of the larger marginal ones 4–6 mm deep, the depth mostly in the narrow V-shaped bottom; carpels 9 (but in a double the carpels 23 and the phalange 8.5 cm wide), the apices of the marginal ones broad and retuse, with a large concavity distal of the stigma; central carpels with apices  $\frac{1}{3}$ – $\frac{1}{2}$  the size of the others, low pyramidal-convex, lacking the apical concavity; stigma 1 mm long, transversely elliptic, flush or oblique, centripetal, creased, brown, papillose, proximal crease deep, usually extending to the valley bottom; endocarp supramedian, bony, dark brown, the lateral walls 3–4 mm thick; seeds 11–15 mm long, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern traversed by several strong fibers; basal mesocarp fibrous and fleshy.

HOLOTYPE: Christmas Island (Indian Ocean), Waterfall, Oct. 1904, *H. N. Ridley* (SING).

*Pandanus Hendersonii* sp. nov. (sect. *Pandanus*)

Fig. 218

DIAGNOSIS HOLOTYPE: Arbor 2.7 m alta, foliis 1.01–1.53 m longis 4–5 cm latis coriaceis supra viridibus infra subpallidioribus supra midnervum sulcatis et cum plicis binis obtusis in sectione mediali cum 38–42 nervis secundariis parallelis in quoque dimidio nervis tertiis non evidentis lamina gladiformata ex basi sensim in apice 15 cm longo trigono subulato diminuenti eo 10 cm ex apice 4 mm lato basi amplexicauli et inermi sed ex 4–5 cm marginibus cum aculeis 1.5–5 mm longis 3–12 mm separatis subulatis pallidis adscendentibus, midnervo infra ex 11 cm cum aculeis 1.5–2.5 mm longis 13–21 mm separatis crassiter subulatis reflexis, in sectione mediali marginibus et midnervo infra cum aculeis 2–2.5 mm longis 4–8 mm separatis subulatis adpresse adscendentibus apicibus brunneis, in apice subulato marginibus et midnervo infra cum serrulis 0.2–0.5 mm longis 1–8 mm separatis, infructescentia pendenti cum syncarpio unico, pedunculo 20 cm et plus longo folioso-bracteato, syncarpio 19 cm longo 11 cm diametro anguste obovoideo-ellipsoideo subtrigono cum 70 phalangibus eis 4.5–5 cm longis 2.8–4 cm latis 2.4–3.4 cm crassis pyriformatis



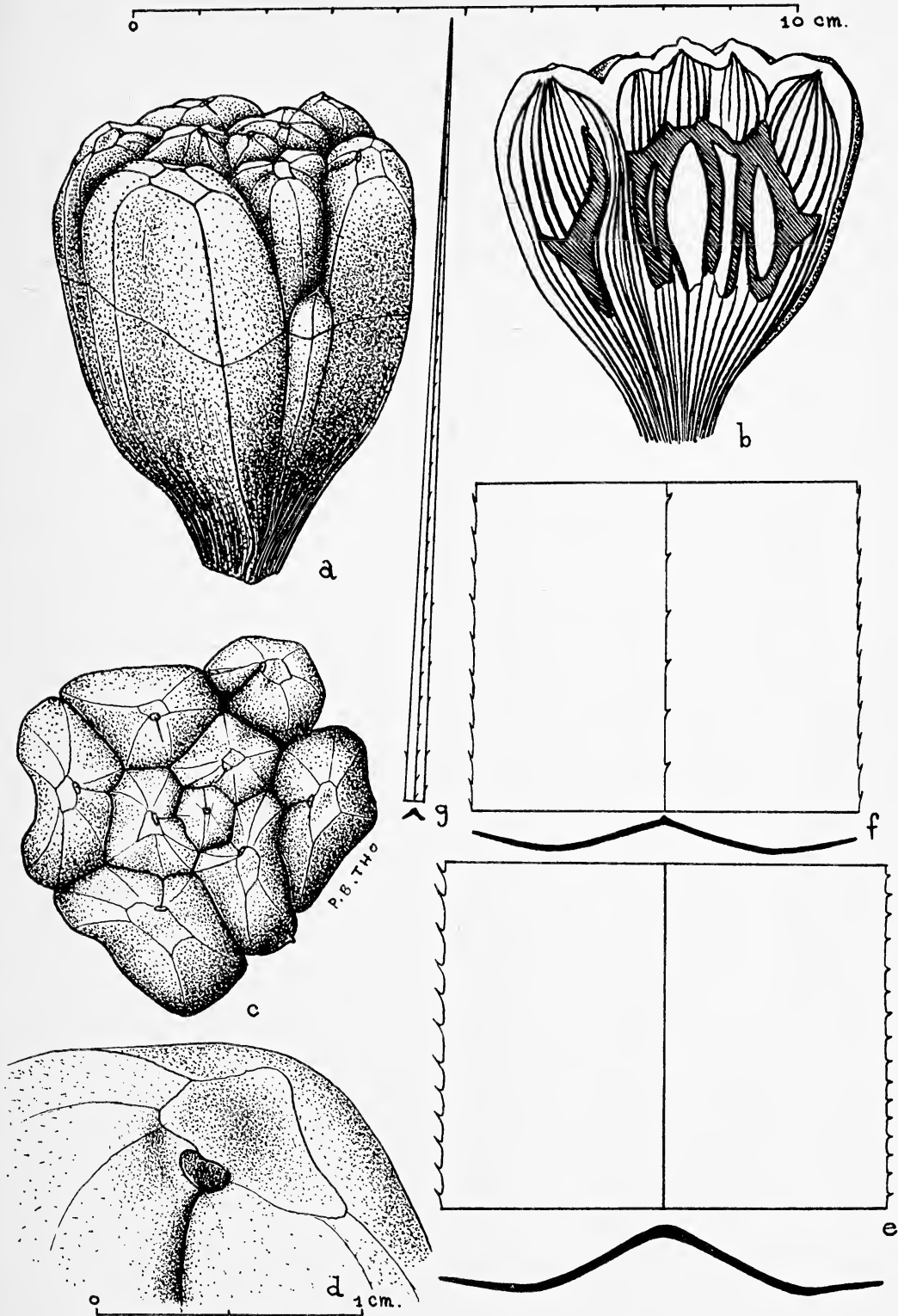


FIG. 217. *Pandanus nativitatis* Ridl., from holotype. *a*, Phalange, lateral view,  $\times 1$ ; *b*, phalange, longitudinal median section,  $\times 1$ ; *c*, phalange, apical view,  $\times 1$ ; *d*, carpel apex, stigma, and proximal sinus,  $\times 4$ ; *e*, leaf base, lower side,  $\times 1$ ; *f*, leaf middle, lower side,  $\times 1$ ; *g*, leaf apex, lower side,  $\times 1$ .

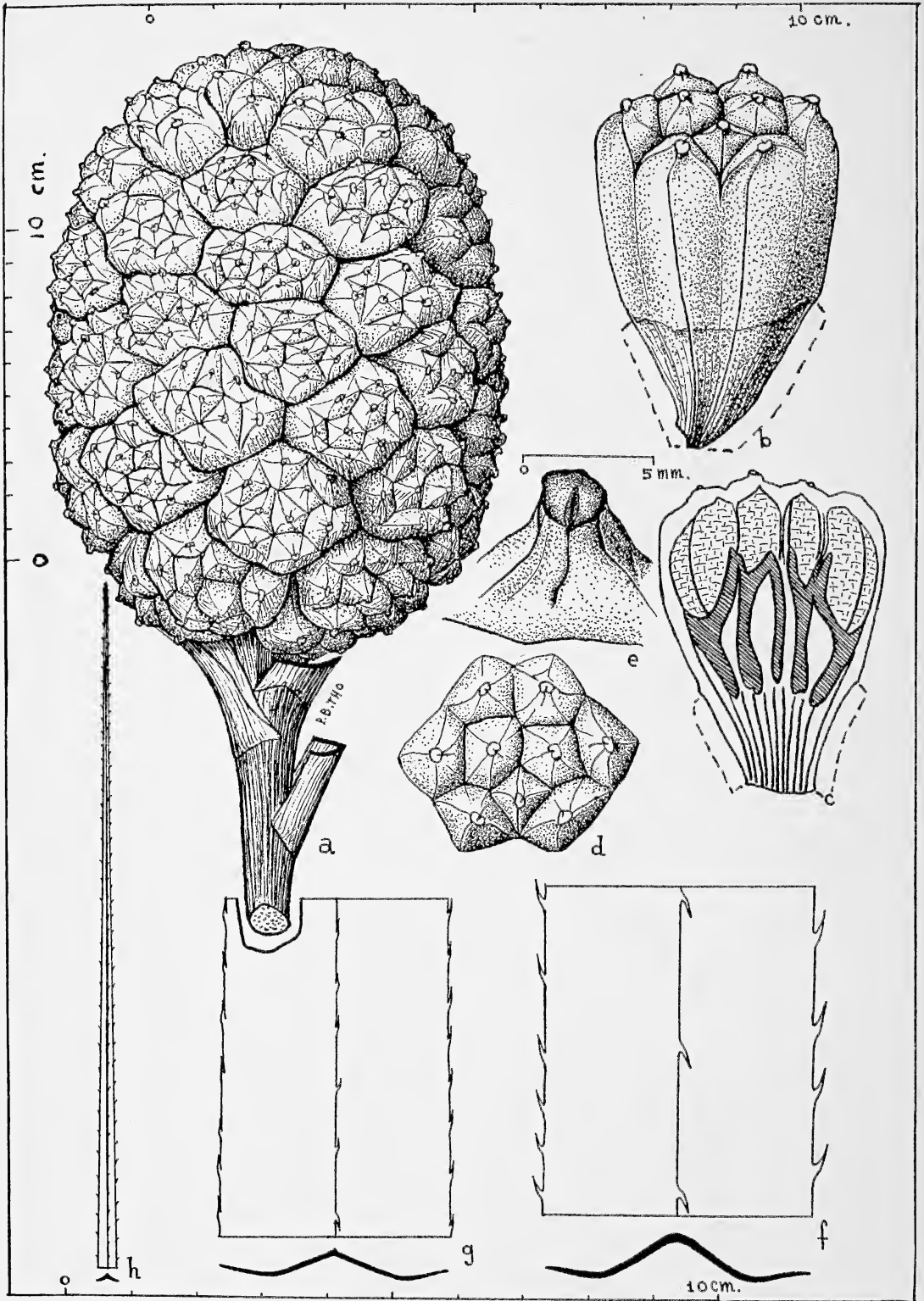


FIG. 218. *Pandanus Hendersonii* St. John, from holotype. *a*, Syncarp,  $\times \frac{1}{2}$ ; *b*, phalange, lateral view,  $\times 1$ ; *c*, phalange, longitudinal median section,  $\times 1$ ; *d*, phalange, apical view,  $\times 1$ ; *e*, carpel apex, stigma, and proximal sinus, oblique view,  $\times 4$ ; *f*, leaf base, lower side,  $\times 1$ ; *g*, leaf middle, lower side,  $\times 1$ ; *h*, leaf apex, lower side,  $\times 1$ .



aurantiaco-rubris et luteis parte  $\frac{3}{5}$  supera libera 5–6-angulosa, apice convexo lateribus subcurvatis vel subplanis laevibus lucidis, suturis lateribus nullis, sinibus centralibus apicalibus 3–4 mm profundis anguste V-formatis in centro recto vel subcurvato, carpelis 7–11 plerumque 8–10 apicibus obtusis vel depresso obtusis pyramidalibus, parte  $\frac{3}{5}$  infera carnosio-incrassata, stigmatibus 2–2.5 mm longis elevatis horizontalibus vel obliquis suborbicularibus vel cordatis vel transverse ellipticis sulcatis brunneis papillosis centripetalibus, sinibus proximalibus latis  $\frac{1}{2}$  ad fondam extensis, endocarpio subsupramediali 2 cm longo osseoso obscure mahoganicolorato lateribus 1.3–1.5 mm crassis intra laevibus lucidis, seminibus 9–11 mm longis ellipsoideis, mesocarpio supero in apice carpelae quaeque cavernam cum membranis albis et fibris paucis formanti, mesocarpio basali fibroso et carnosio.

**DESCRIPTION OF ALL SPECIMENS EXAMINED:** Treelike, 2.7 m tall; leaves 1.01–1.53 m long, 4–5 cm wide, coriaceous, green above, slightly paler green below, furrowed above the midrib, with 2 rounded lateral pleats, at midsection with 38–42 secondary parallel veins in each half, tertiary veins not evident, blade sword-shaped, tapering gradually from the base to the 15 cm trigonous subulate apex, this 10 cm down 4 mm wide, the base amplexicaul and unarmed, pale, but beginning 4–5 cm up the margins with prickles 1.5–5 mm long, 3–12 mm apart, subulate, ascending, pale; the midrib below beginning at 11 cm with prickles 1.5–2.5 mm long, 13–21 mm apart, stout arcuate subulate, reflexed; at midsection the margins and midrib below with prickles 2–2.5 mm long, 4–8 mm apart, subulate, appressed ascending, brown-tipped; on the subulate apex the margins and midrib below with serrulations 0.2–0.5 mm long, 1–8 mm apart; infructescence pendent, with one syncarp; peduncle 20 cm or more in length, leafy bracted; syncarp 19 cm long, 11 cm in diameter, narrowly obovoid-ellipsoid, perceptibly 3-sided, bearing 70 phalanges, these 4.5–5 cm long, 2.8–4 cm wide, 2.4–3.4 cm thick, pyriform, orange-red and yellow, upper  $\frac{3}{5}$  free and 5–6-angled, the apex convex, the sides gently curved or almost plane, smooth, shining, lateral sutures none; central apical sinuses 3–4 mm deep, narrow V-shaped only at the center,

straight or gently curved; carpels 7–11, mostly 8–10, the apices from obtuse to low obtuse pyramidal; lower  $\frac{3}{5}$  of phalanges fleshy enlarged, as shown by the persistent shoulders; stigmas 2–2.5 mm long, elevated, horizontal or oblique, suborbicular, cordate, or transversely elliptic, creased, brown, papillose, centripetal; proximal sinus wide, running  $\frac{1}{2}$  way to valley bottom; endocarp slightly supramedian, 2 cm long, bony, dark mahogany-colored, the lateral walls 1.3–1.5 mm thick, the inner surfaces smooth, shining; seeds 9–11 mm long, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with an aerenchyma of white membranes and a few fibers; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Indonesia, Anamba Islands, Padang, near Letong, Jemoja, sea level, 12 April 1928, *M. R. Henderson* 20,365 (SING). Isotypes (BO, K)!

**SPECIMENS EXAMINED:** Anamba Islands, Tanjong Suka, Siantan, among rocks near sea, 5 April 1928, *M. R. Henderson* 20,222 (K, SING).

**DISCUSSION:** *P. Hendersonii* is a member of the section *Pandanus*, as is its closest relative, *P. rubricoloratus* St. John, from Pulau Tioman, off the east coast of Malaya. The latter species has the syncarp 9 cm long, globose; phalanges 3.6 cm long, red, the central apical sinuses 0.5–2 mm deep; endocarp inner surfaces papillose and a little shiny; leaves 66–73 cm long, 2.8–3 cm wide, at midsection with 27 secondary parallel veins in each half and the midrib below with prickles 1.5–2 mm long, 6–13 mm apart, *P. Hendersonii* has the syncarp 19 cm long, obovoid-ellipsoid; phalanges 4.5–5 cm long, orange-red and yellow; central apical sinuses 3–4 mm deep; endocarp inner surfaces smooth, shining; leaves 1.01–1.53 m long, 4–5 cm wide, at midsection with 38–42 secondary parallel veins in each half, and the midrib below with prickles 2–2.5 mm long, 4–8 mm apart.

The second collection, Henderson 20,222, is identical with the type except for having a smaller syncarp with smaller phalanges (about 3.9 cm long). From their structure and appearance, this difference is judged to be due to immaturity.

This new species is named in honor of *M. R. Henderson*, former director of the Singapore Botanic Garden.



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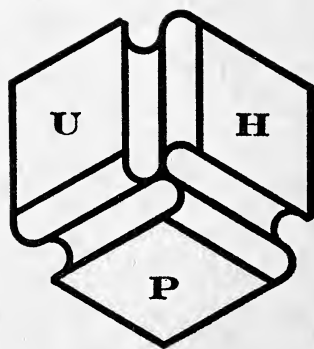
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# PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL  
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*A New Species of Pachycerianthus*

G. BROWNLIE

*Geographical Affinities of South Pacific Fern Floras*

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*Revision of the Genus Pandanus*

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# The Sponges of Micronesia, Part I

## The Palau Archipelago

PATRICIA R. BERGQUIST<sup>1</sup>

ALTHOUGH potentially interesting from a zoogeographic standpoint, the marine fauna of the Palau Islands and of the islands and atolls to the eastward, with the exception of Hawaii, have received scant attention from expeditions and individual collectors. It was to repair this gap in our knowledge that the "Project Coral Fish" expeditions to the western and central Pacific were undertaken. The first of these expeditions visited the Palau Islands in 1955 and made extensive marine collections, of which the sponges described below were a part.

Previous work relating to the Demospongiae of the Palau Islands is restricted to de Laubenfels' (1954) "Sponges of the West Central Pacific." This monograph was based upon the author's own collections in the Caroline Islands, Marshall Islands, and the Marianas; and it contains, in addition to descriptions of many new species, significant field observations which have facilitated identification of the present collection. There are 33 species common to the two collections and the identification of these has necessitated considerable revision of portions of de Laubenfels' monograph.

The Palau Islands belong to the Western Caroline group and are situated on a submarine ridge running northeast from the Moluccas at 6° 53' N to 8° 06' N, 134° 29' E. Between the Palaus and the Philippines is the Philippine Trench, which acts as an effective natural barrier to the free migration of shallow-water invertebrates. Consequently, zoogeographic interest in the Palau area focuses on whether the fauna has remained similar to that of the Indo-Malayan region, through interchange of populations across the intervening 600 miles, or has diverged significantly, producing a high percentage of endemic species.

In order to generalize about the relationships of the Palau Islands sponge fauna it is necessary to know something of the faunas of contiguous areas. Two main regions have contributed to the Palauan fauna, the Indo-Malayan and the New Guinea-northern Australian. The sponge fauna of the Indo-Malayan region is known chiefly from the works of Thiele (1898, 1900, 1903), Lindgren (1897), Kieschnick (1898), Topsent (1897), Henschel (1912), Wilson (1925), de Laubenfels (1935), and Lévi (1961).

Islands to the east of the Palaus are relatively unknown in respect to their sponge fauna. With the exception of Hawaii the literature is restricted to Kirkpatrick (1900) for Christmas Island; and de Laubenfels (1949) for Yap, (1955) for Onotoa, and (1954) for the Marshall Islands, Caroline Islands, and the Marianas.

Our knowledge of the New Guinea and northern Australian fauna stems from the work of Ridley (1884) and Burton (1934).

Many of the references cited above are very old and require extensive revision; this, added to the obvious incompleteness of the faunal picture they present of their respective areas, restricts the zoogeographic comparisons that can be made. In view of the unreliability of the literature, the statements made here with respect to the Palau Islands are based solely on the specimens examined in the course of this investigation, and draw on de Laubenfels' work only where this has been verified. It will be possible to give a more detailed analysis when collections from Ifaluk, Kapingamarangi, the Philippines, and Hawaii have been fully studied.

Fifty species are described in this report; of this number nine are new. A total of 14 species is endemic to the Palau Islands; seven species are known only from the Palaus eastward, in the case of *Xestospongia exigua* eastward to

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Christmas Island. Thirteen species are common to the Indo-Malayan and Palau areas, extending, in the case of *Iotrochota baculifera*, *Clathria fasciculata*, *Clathria cervicornis*, *Neofolitispa dianchora*, and *Asteropus sarasinorum*, eastward to the Marshall Islands. Eleven species have a wide Indo-Pacific distribution: *Heteronema erecta*, *Ircinia ramosa*, *Phyllospongia foliascens*, *Psammaphysilla purpurea*, *Dysidea herbacea*, *Coelocarteria singaporense*, *Myrmekioderma granulata*, *Spirastrella vagabunda*, *Placospongia melobesioides*, *Ancorina acervus*, and *Cinachyra australiensis*. Three species are known elsewhere only from Australia, in the case of *Jaspis coriacea* only from South Australia.

The sponge fauna of the Palau Islands is certainly richer and more varied than that of any of the more easterly islands thus far studied. It is not possible, however, to compare the quantity and variety of Demospongiae in Indo-Malayan localities with that of the Palau Islands without more data on both areas.

The broad system of classification used in this work is basically that propounded by Topsent (1928) and modified by de Laubenfels (1936). In several cases minor alterations in this system have been suggested. The Axinellidae are still treated as a family of the Halichondrida, although it is clear that they should be elevated to the level of a separate order. To reassign the genera involved is a long task, the material for which is not immediately available.

Throughout the text means are given in parentheses with the range of spicule dimensions.

All color notations are after Munsell's *Book of Color*.

#### ACKNOWLEDGMENTS

The author is greatly indebted to Dr. W. D. Hartman for his advice and assistance throughout the preparation of this manuscript.

Mr. R. Binkowski is thanked for technical assistance, Mr. J. Howard for photographic work, and Mrs. Shirley Hartman for the preparation of all drawings.

This research was made possible by the award of a Sessel Fellowship in Bio'logy from Yale University and by National Science Foundation Grant GB-516 to Yale University.

#### STATION DATA

- Sta. 10. Madalai district, west end of Koror I., Abé's Traverse III. Sand bottom with *Enhalus* and *Halimeda*; depth 12 inches at low water. July 8, 1955.
- Sta. 12. Madalai district, west end of Koror I., Abé's Traverse II, at south end of Koror-Arakabesan Causeway. Mud and sand, with *Enhalus*, *Halimeda* and *Padina*; exposed at low water. July 9, 1955.
- Sta. 15. Madalai district, west end of Koror I. Shallow flat enclosed by retaining wall parallel to Malakal Causeway. Sand and silt, with *Enhalus*; depth 18-24 inches at low water. July 11, 1955.
- Sta. 25. Inner margin of barrier reef, 8 miles NW of Koror. Sand, coral, dead coral blocks; depth 3-7 ft. July 19, 1955.
- Sta. 35. Peleliu boat channel, between Ngargersal and Kongauru islands, ca. 1 mile east of north tip of Peleliu. Sand, silt, some coral; *Enhalus acoroides* and 2 other species of eel-grass; algae incl. *Caulerpa* spp. Depth 1-10 ft. July 24, 1955.
- Sta. 47. Iwayama Bay, shore of islands XXXIII and XXXIV, west side of Kogai-Hanto. Sand, live and dead coral; *Enhalus* in sand, *Padina* on rocky areas. July 28, 1955.
- Sta. 53. Ngaremdiu area, eastern Urukthapel; rocky cape west of sand beach Oiratel-ruul. Sand, coral, rock; small eel grass and *Halophila ovalis*; depth 0-7 ft. July 31, 1955.
- Sta. 59. Reef bordering eel grass flat east of Ebadul's dock, north shore of Koror. Living and dead coral, with sparse patches of sand. Aug. 4, 1955.
- Sta. 50. Sand and eel grass flat west of Ebadul's dock, north shore of Koror. Sand with occasional coral patches, *Enhalus* abundant, long streamers of sargassum attached to dead coral. August 5, 1955.
- Sta. 61. Seaward reef flat at south end of Nge-melis I., west side of Palau Archipelago. Coral and sand, some *Enhalus* and *Halimeda* in sand patches; depth 18 inches-6 ft. August 6, 1955.
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- Sta. 67. Reef in pass west of Nghus ("Ankosu" on charts), southern tip of Urukthapel. Living and dead coral, sand, coral rubble; depth 5–7 ft. Aug. 7, 1955.
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- Sta. 100. Iwayama Bay, Bay of the Dragon Palace, west side of Kogai-hanto. Bottom coral, sand in pockets; depth 5–15 ft. August 16, 1955.
- Sta. 104. Malakal Harbor. From sunken ship off north shore of Urukthapel; depth 40–50 ft. August 17, 1955.
- Sta. 106. Reef flat, Ngadarak reef north of mouth of Malakal Pass. Exposed coral rubble with residual tide pools. August 17, 1955.
- Sta. 111. Reef flat, Ngaremdiu reef, east side of Urukthapel. Exposed boulder flat. August 19, 1955.
- Sta. 124. Yoo Passage, west of Kasao Reef,  $3\frac{1}{4}$  miles SSE of Ngaremdiu, east side of Urukthapel. August 24, 1955 [Gloria Maris Sta. 450, haul 2].
- Sta. 125.  $1\frac{3}{4}$  miles NE of Ngabadangel (Cape "Gabadaguru" on charts). Sand with *Halimeda* and *Seriatopora*, 17 fms. August 24, 1955. [Gloria Maris Sta. 452, haul 1].
- Sta. 133. Iwayama Bay, south shore of island II. Reef flat between shore and deep reef pool; area of Abé's traverses VIII, IX, and X. Coral with sand pockets; depth 2–3 ft at m.l.w. August 28, 1955.
- Sta. 134. Iwayama Bay, south end of island XX. Reef shelf and slope; bottom entirely coral and rock; depth 3–20 ft. August 28, 1955.
- Sta. 135. Iwayama Bay, west side of island XXII. Reef shelf and slope; bottom entirely coral and rock; depth 3–40 ft. August 28, 1955.
- Sta. 136. Reef flat outside of large cave at SE end of Koror, east entrance of Iwayama Bay. Sand, branched coral (*Montipora*, *Seriatopora*), and vegetation (*Enhalus*, *Halimeda*, *Padina*); depth 4–6 ft. August 28, 1955.
- Sta. 140. Iwayama Bay, in Ngerchelngael ("Geruherugairu" on charts) Pass, between Kogai Peninsula and Kaibakku I. *Montipora*-flat with *Enhalus*, *Halimeda*, *Padina*, and some rocks of foreign origin; depth 4–5 ft. August 30, 1955.
- Sta. 219. Iwayama Bay (Abé's Division L), extreme eastern part. Marginal reef along coast of Koror called U'lamii' (or Uchlamiich). Living and dead coral, sand patches; depth 3–20 ft. October 12, 1955.
- Sta. 220. Iwayama Bay, east side of mouth of Kaki-suido (Oyster Pass) between islands XXIX and SE Koror. Limestone, live and dead coral; depth 3–20 ft. October 12, 1955.
- Sta. 220A. Same as 220 but collected Oct. 22, 1955.
- Sta. 220B. Same as 220 but collected Oct. 29, 1955.
- Sta. 236A. Same as 220 but 150 yds. north. Oct. 20, 1955.
- Sta. 245. West shore of Urukthapel, in small bay;  $7^{\circ} 16' 31''$  N,  $134^{\circ} 26' 13''$  E. Limestone shelf, coral, *Halimeda*, 3–10 ft. October 23, 1955.
- Sta. 252. Fringing reef of small island in west part of lagoon of Eil Malk Island. Limestone, coral, sand, 0–10 ft. October 27, 1955.
- Sta. 258. Small bay in north coast of Ngaremdiu region of Urukthapel, near Japanese stone pier. Sand, live and dead coral, limestone, with *Enhalus* and *Halimeda*, much stinging *Stephanoscyphus*; depth 2–4 ft. November 2, 1955.

#### SYSTEMATIC DESCRIPTION AND DISCUSSION (Species included are listed in systematic order)

##### Order Keratosa Grant

##### Suborder Dictyoceratida Minchin

##### Family Spongiidae Gray

##### Genus *Spongia* Linné

##### *Spongia officinalis* Linné

##### Genus *Dactylospongia* n. gen.

##### *Dactylospongia elegans* (Thiele)

##### Genus *Heteronema* Keller

##### *Heteronema erecta* Keller

##### Genus *Ircinia* Nardo

##### *Ircinia ramosa* Keller

##### Genus *Phyllospongia*

##### *Phyllospongia foliascens* (Pallas)

##### *Phyllospongia dendyi* Lendenfeld

##### Genus *Fasciospongia* Burton

##### *Fasciospongia chondrodes*

##### (de Laubenfels)

Genus *Psammaplysilla* Keller  
*Psammaplysilla purpurea* Carter

Family Dysideidae Gray

Genus *Dysidea* Johnston  
*Dysidea herbacea* (Keller)  
*Dysidea chlorea* de Laubenfels  
*Dysidea granulosa* n. sp.  
*Dysidea arenaria* n. sp.

Genus *Euryspongia*  
*Euryspongia lobata* n. sp.

Order Haplosclerida Topsent

Family Haliclonaidae de Laubenfels

Genus *Haliclona* Grant  
*Haliclona velinea* (de Laubenfels)  
*Haliclona koremella* de Laubenfels

Genus *Cribrochalina* Schmidt  
*Cribrochalina olemda* de Laubenfels

Genus *Xestospongia* de Laubenfels  
*Xestospongia exigua* (Kirkpatrick)

Family Callyspongiidae de Laubenfels

Genus *Callyspongia* Duchassaing and Michelotti  
*Callyspongia subarmigera* (Ridley)  
*Callyspongia ridleyi* Burton

Family Desmacidonidae Gray

Genus *Gelliodes* Ridley  
*Gelliodes gracilis* Hentschel

Order Poecilosclerida Topsent

Suborder Phorbasiformes de Laubenfels

Family Adocidae de Laubenfels

Genus *Adocia* Gray  
*Adocia turquosia* de Laubenfels

Genus *Toxadocia* de Laubenfels  
*Toxadocia violacea* de Laubenfels

Genus *Orina* Gray  
*Orina sagittaria* Sollas

Genus *Kallypilidion* de Laubenfels  
*Kallypilidion poseidon* de Laubenfels

Genus *Pellina* Schmidt  
*Pellina carbonaria* (Lamarck)

Genus *Siphonodictyon* n. gen.  
*Siphonodictyon mucosa* n. sp.

Family Coelosphaeridae Hentschel

Genus *Coelocartheria* Burton  
*Coelocartheria singaporense* (Carter)

Suborder Myxilliformes de Laubenfels

Family Tedaniidae Ridley and Dendy

Genus *Iotrochota* Ridley  
*Iotrochota baculifera* Ridley

Suborder Microcioniformes de Laubenfels

Family Microcionidae Hentschel

Genus *Microciona* Bowerbank  
*Microciona eurypta* (de Laubenfels)

Genus *Clathria* Schmidt  
*Clathria cervicornis* (Thiele)

*Clathria fasciculata* Wilson

Family Ophlitaspongiidae de Laubenfels

Genus *Mycale* Gray  
*Mycale lissochela* n. sp.  
*Mycale cavernosa* n. sp.

Genus *Neofolitispa* nom. nov.

*Neofolitispa dianchora*  
(de Laubenfels)

Genus *Desmacella* Schmidt

*Desmacella lamprea* de Laubenfels

Order Halichondrida Topsent

Family Axinellidae Ridley and Dendy

Genus *Pseudaxynissa* Burton  
*Pseudaxynissa pitys* de Laubenfels

Genus *Phycopsis* Carter  
*Phycopsis* sp. cf. *terpnis* de Laubenfels

Family Desmoxiidae Hallmann

Genus *Higginsia* Higgin  
*Higginsia mixta* (Hentschel)

Genus *Myrmekioderma* Ehlers  
*Myrmekioderma granulata* (Esper)

Order Hadromerida Topsent

Family Spirastrellidae Hentschel

Genus *Spirastrella* Schmidt  
*Spirastrella aurivilli* Lindgren

*Spirastrella vagabunda* Ridley

Genus *Timea* Gray  
*Timea granulata* n. sp.

Family Placospongiidae Gray

Genus *Placospongia* Gray  
*Placospongia melobesioides* Gray

Order Epipolasida Sollas

Family Jaspidae de Laubenfels

Genus *Asteropus* Sollas  
*Asteropus sarasinorum* (Thiele)

Genus *Jaspis* Gray  
*Jaspis coriacea* (Carter)

Order Choristida Sollas

Family Ancorinidae Gray

Subfamily Ancorininae de Laubenfels

Genus *Ancorina* Schmidt  
*Ancorina acervus* (Bowerbank)

## Subfamily Stellettinae Sollas

Genus *Stelletta* Schmidt*Stelletta durissima* n. sp.

## Family Tetillidae Sollas

Genus *Tetilla* Schmidt*Tetilla microxea* n. sp.Genus *Paratetilla* Dendy*Paratetilla bacca* (Selenka)Genus *Cinachyra* Sollas*Cinachyra australiensis* (Carter)  
(complex of species)

## ORDER KERATOSA Grant

## SUBORDER DICTYOCERATIDA Minchin

## FAMILY SPONGIIDAE Gray

GENUS *Spongia* Linné*Spongia officinalis* Linné, 1759, p. 1348, pl. 1,

## RESTRICTED SYNONYMY:

*Spongia officinalis* Linné, 1759, p. 1348, pl. 1,  
figs. 1 and 2.*Spongia officinalis* subspecies *matamata* de  
Laubenfels, 1954, p. 4.

OCCURRENCE: Sta. 60.

REMARKS: A single specimen of this sponge  
is in the present collection. It compares well  
with the type of de Laubenfels' *S. officinalis*  
subspecies *matamata*, USNM 23200, except that  
the primary fibres are stouter, up to 80 $\mu$  in  
diameter, and more frequent than is inferred  
in de Laubenfels' (1954) description.Embryos in all stages of segmentation are  
present in the specimen, and the older embryos  
are very darkly pigmented.No attempt is made here to evaluate the pre-  
vious records of *Spongia officinalis* from the  
Indo-Pacific region. It is evident that systematic  
relationships are confused in the entire genus  
and particularly in *S. officinalis* and *S. zimocca*.  
A careful study of more extensive collections  
than are presently available is necessary before  
affirming that all specimens referred to these  
species are correctly assigned.DISTRIBUTION: Mediterranean, West Indies,  
Australia, Indian Ocean, Norway(?), South  
America, Marshall Islands.GENUS *Dactylospongia* nov. gen.Dictyoceratida with skeleton a relatively reg-  
ular network of polygonal meshes without dif-  
ferentiation into ascending and connecting ele-  
ments. Fibres lack foreign inclusions except for  
a few isolated spicule fragments, have a granu-  
late surface texture and a faintly stratified struc-  
ture. The sponge surface is free of detritus and  
is covered with irregular conules. The dermal  
membrane between rows of conules is stretched  
over deep subdermal channels which extend for  
a considerable vertical distance. Flagellate cham-  
bers are evenly distributed throughout the endo-  
some, and are spherical and small, 24–30 $\mu$  in  
diameter. The genus is erected for the type spe-  
cies, *Luffariella elegans* Thiele, and is most  
closely allied to *Hippospongia*.*Dactylospongia elegans* (Thiele)

Fig. 1a, b

*Luffariella elegans* Thiele, 1899, p. 25, pl. 3,  
fig. 4, pl. 5, fig. 20.

OCCURRENCE: Sta. 47. Palau Islands.

DESCRIPTION: Several pieces of this sponge  
were obtained, probably all from one large col-  
ony with long thin anastomosing branches di-  
verging from a small poorly defined basal  
region. The branches are 0.5–1.5 cm wide, up  
to 32 cm long, and many have several anasto-  
moses along their length.COLOR: In alcohol, dark reddish-brown, be-  
tween (rY-R2/2) and (rY-3/2).TEXTURE: Extremely tough and elastic, al-  
most rubbery.SURFACE: Coarsely conulose, with the conules  
tending to be aligned in rows between which  
the dermal membrane is stretched. In parts of  
the sponge the dermal membrane of either sur-  
face is all that connects two adjacent branches.  
In the preserved sponge the membrane is  
sunken into deep subdermal cavities which may  
be up to 4.0 cm long and 0.5 cm wide. Conules  
are irregular, squarish, multituberculate, and  
up to 0.5 cm long, 0.2 cm high, and 0.2 cm  
wide. The oscules are distributed irregularly  
over the surface of the branches and are 0.08–  
0.2 mm in diameter. Pores are absent from the  
areas where the dermal membrane extends over

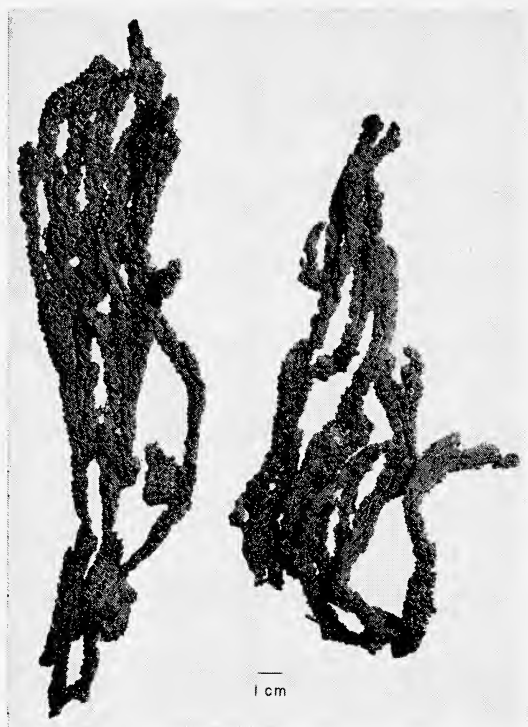


FIG. 1a. *Dactylospongia elegans* (Thiele). USNM 23707.

subdermal cavities, but abundant over most of the surface.

**SKELETON:** A compact irregular reticulation of clear yellow-brown fibres; many ascending fibres are distinguishable only immediately below the surface. Some stratification is shown in most fibres and a poorly demarcated pith occurs infrequently. Isolated spicule fragments occur randomly. A characteristic feature of the skeleton is the granulate surface of the fibres. Fibre diameter is  $20\text{--}54\mu$  ( $38\mu$ ).

**FLAGELLATE CHAMBERS:** Small, spherical,  $24\text{--}30\mu$  in diameter, and are regularly distributed throughout the body of the sponge except in the lacunar areas which surround the subdermal cavities. The endosome contains many darkly pigmented granules and abundant diatom skeletons.

**DISCUSSION:** Thiele (1899) described this sponge from the Celebes and established the genus *Luffariella* to receive *Luffaria variabilis* Poléjaeff and *Luffariella elegans*; the former was designated as the type of the genus by Thiele and later by de Laubenfels (1936).

Considerable confusion has centered around the correct generic position of *Luffaria variabilis*. The genus *Luffaria* was unrecognizably described by Duchassaing and Michelotti (1864). Schmidt (1870) redescribed the genus without adding any species, and Poléjaeff (1884) described *Luffaria variabilis*. Lendenfeld (1889) recognized that Poléjaeff's sponge was not a *Luffaria* as understood by Schmidt (= *Verongia*), and took the erroneous step of re-establishing *Luffaria* under Poléjaeff's name to receive *L. variabilis* and two new species. Topsent (1934) considered that both *Luffaria* and *Luffariella* should be abandoned and all species involved transferred to *Aplysinopsis* Lendenfeld. The difference between *Aplysinopsis* and *Thorecta* Lendenfeld is very slight, merely that *Thorecta* has a relatively smooth surface and more foreign material in the dermis (see de Laubenfels, 1948). These two genera are now considered synonymous.

The type specimen of *Luffaria variabilis* Poléjaeff should be established as BM 85.8.52. This sponge has been examined and in most features it is compatible with *Cacospongia*. It has, however, one distinguishing characteristic: an extremely fine and regular tertiary fibre network is present throughout the sponge. In view of this marked difference in the skeleton, it is proposed to retain *Luffariella* for *L. variabilis* and other sponges which have comparable skeletal structure. *Luffariella geometrica* Kirkpatrick may properly belong here.

It is clear that *Luffariella elegans* Thiele is generically distinct from *Luffariella variabilis*.

Examination of the Palau specimen of *L. elegans* and an undescribed specimen in the British Museum (1946.11.25.170) shows that the correct generic grouping for this sponge is not near *Cacospongia* but near *Hippospongia*, differing from some specimens of this genus only in form, the presence of long surface channels, and the lack of any cored primary fibres. These are the only features separating *L. elegans* and *Hippospongia metachromia*<sup>2</sup> (de Laubenfels), also from the Palau Islands.

<sup>2</sup> No cored ascending fibres were described for this sponge, but re-examination of the type has shown them to be present in the subdermal region.

Since the genus *Luffariella* is retained for *L. variabilis*, a new genus *Dactylospongia* is erected to receive *Luffariella elegans*.

DISTRIBUTION: Celebes (Thiele)

#### GENUS *Heteronema* Keller

##### *Heteronema erecta* Keller

Fig. 2

*Heteronema erecta* Keller, 1889, p. 339.

*Heteronema erecta* Row, 1911, p. 369.

*Thorectopsamma mela* de Laubenfels, 1954, p. 29, fig. 15, pl. 8, fig. 6.

*Thorectopsamma mela* de Laubenfels, 1955, p. 138.

OCCURRENCE: Sta. 10, 100, 140.

DESCRIPTION: De Laubenfels (1954) has given an excellent description of this sponge as it occurs in the Micronesian area and little can be added except to note that: (1) the primary fibres have a tendency to be fasciculated immediately below the surface; (2) The dermis is crowded with granules containing a black pigment; (3) The immediate subdermal region is cavernous, consequently the dermis is easily detachable; and (4) The pigment granules in the subdermal and deep layers of the body are extremely abundant and tend to obscure the chambers and canal system.

DISCUSSION: Comparison of Red Sea specimens of *Heteronema erecta* with de Laubenfels' Pacific sponges identified as *Thorectopsamma mela* reveals that the two species are identical. The extremely characteristic surface pattern of radiating ridges between conules is present in all specimens examined from both geographical areas. The texture of the sponge varies greatly: some of the Palau specimens are relatively compressible; others are extremely hard and thus compare with specimens described by Row (1911).

With the removal of *T. mela* to *Heteronema*, the genus *Thorectopsamma* Burton is reduced to three species. *T. irregularis*, the type species, was described from a single specimen; it had laminated fibres densely packed with debris and no special dermal skeleton. Burton made no mention of the soft tissues of his sponge. Re-examination of the type of *T. irregularis* (BM 30.8.13.217) shows that the flagellate chambers

are small and spherical, 20–30 $\mu$  in diameter; the subdermal region is extremely cavernous and darkly pigmented. This sponge is not easily distinguishable from *Heteronema*.

The second species described in *Thorectopsamma* is *T. chromogenia* de Laubenfels from Bermuda. This sponge is a dark red color and has far less debris in the fibres than *T. irregularis*. The flagellate chambers were undescribed and apparently much sand was incorporated in the body of the sponge. It is unlikely that this sponge belongs to *Thorectopsamma* but, in view of our incomplete knowledge of its anatomy, no suggestion can be made about its real affinities. *Thorectopsamma xana* de Laubenfels (1954) is referred to *Psammaphysilla purpurea*.

DISTRIBUTION: Red Sea (Keller, Topsent, Row); West Central Pacific; Hawaii (de Laubenfels).

#### GENUS *Ircinia* Nardo

##### *Ircinia ramosa* (Keller)

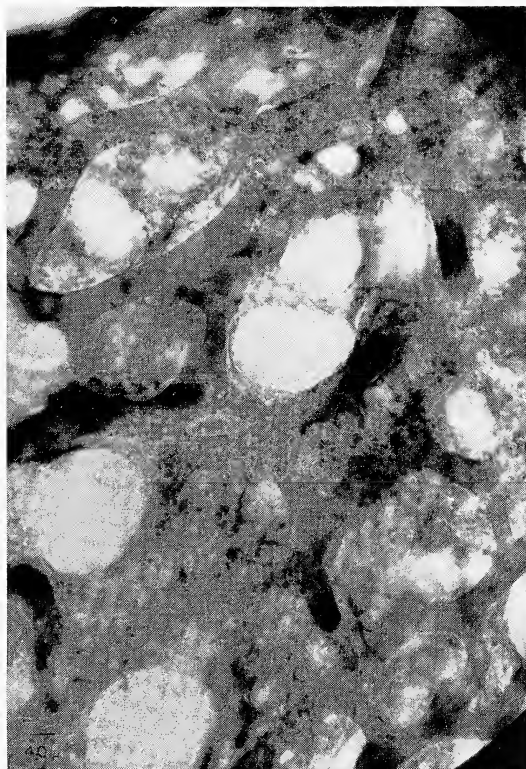


FIG. 1b. *Dactylospongia elegans* (Thiele). Portion of the fibre network.



## RESTRICTED SYNONYMY:

*Hircinia ramosa* Keller, 1889, p. 345, pl. 20, fig. 5.

*Ircinia ramosa* de Laubenfels, 1948, p. 73.

*Ircinia ramosa* de Laubenfels, 1954, p. 23, fig. 11.

OCCURRENCE: Sta. 15, 60, 92.

REMARKS: De Laubenfels (1954) gives a relatively detailed description of this species and stresses the ramose form, the abundant fine filaments, and the presence of a second coarser type of filament containing refractile material as the characteristic features. The specimens in this collection agree in most details with the above. The fibres lacking granules have a greater range in diameter,  $2.0\text{--}5.0\mu$ , than either de Lau-

benfels', or Keller's specimens; the flagellate chambers range from  $24\text{--}36\mu$  in diameter.

De Laubenfels (1950) differentiates *I. ramosa*, in the West Indies, from *I. fasciculata* by the form of the branch tips, rounded in *ramosa*, pointed in *fasciculata*. Hartman (1959) has emphasized the presence of a dermal reticulum of sand grains in *I. ramosa*. At present it is impossible to be sure that the Pacific sponges discussed above belong to the same species as West Indian sponges also named *I. ramosa*; the same problem applies to *I. fasciculata*. In the case of *ramosa*, however, the Pacific sponges seem closer to Keller's original description and, in the event some specific difference is found, the West Indian population would require a new

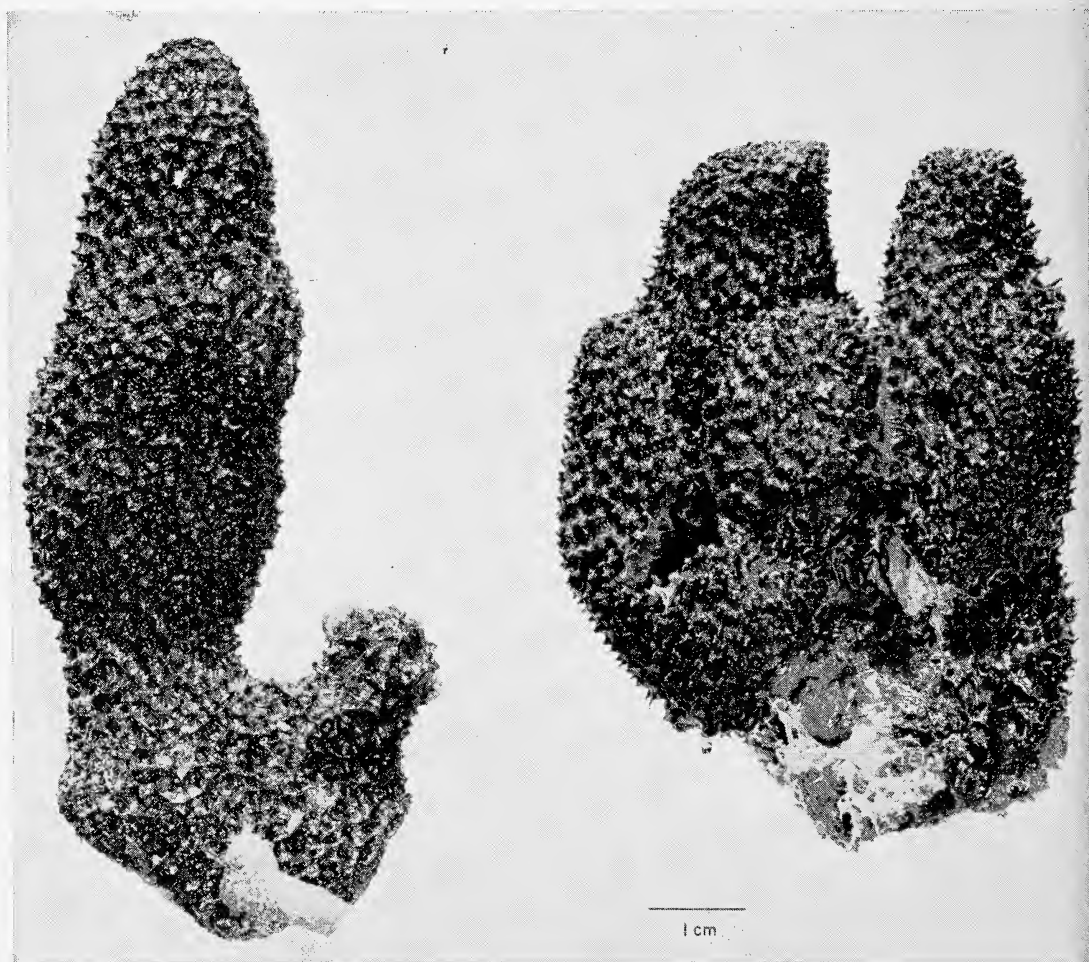


FIG. 2. *Heteronema erecta* Keller. Left, Sta. 10; right, Sta. 140.





FIG. 3a. *Phyllospongia foliascens* (Pallas). Sta. 111.

specific name. It is difficult to see what characters can be used to distinguish between such sponges as *I. ramosa*, *I. fasciculata*, and *I. dendroides* since the entire genus is extremely uniform in internal morphology and, seemingly, variable in habit and surface characteristics. Studies of the ecology and morphology of living populations are urgently required in this genus.

DISTRIBUTION: Red Sea, West Indies, Palau Islands, Ponape, Great Barrier Reef.

GENUS *Phyllospongia* Ehlers

*Phyllospongia foliascens* (Pallas)

Fig. 3a, b

RESTRICTED SYNONYMY:

*Spongia foliascens* Pallas, 1766, p. 395.

*Phyllospongia foliascens* Lendenfeld, 1889, p. 196, pl. v, fig. 3; pl. vi, figs. 1, 3, 4, 10; pl. vii, fig. 11; pl. xiv, fig. 2; pl. xxiv, fig. 6.

*Carteriospongia foliascens* Burton, 1934, p. 573.

*Phyllospongia lekanis* de Laubenfels, 1954, p. 15, fig. 7, pl. 111, fig. a.

OCCURRENCE: Sta. 111, 220A, 245.



FIG. 3b. *Phyllospongia foliascens* (Pallas). Upper, Sta. 245; lower, Sta. 220A.

DESCRIPTION: Three of the five specimens are similar in form to *P. foliascens* as illustrated by Lendenfeld (1889:pl. 5, fig. 3), one is almost identical to *P. lekanis* de Laubenfels (1954:pl. 111, fig. a), and one, of spiral shape, answers to de Laubenfels' description of large specimens of *P. lekanis* which he observed in the field. There is a great variation in the surface ornamentation, and in the distribution and abundance of oscules. In all specimens the skeleton is compact, with cored primary tracts and thick sand cortex on both surfaces. In this respect the present specimens contrast with the holotype of *P. lekanis* (USNM 23109), which has a loose skeleton mesh, lightly cored fibres, and a thin sand cortex on both surfaces.

Little note has been taken in the systematics of *Phyllospongia* of the amount of debris present in the cortex and the skeleton; this, in conjunction with the range of form exhibited by this sponge in the Palaus, is sufficient reason for relegating *P. lekanis* to *P. foliascens*.

DISCUSSION: It is with some hesitation that these specimens are described as *Phyllospongia*

rather than *Carteriospongia*. It seems that *Spongia foliascens* Pallas, which is the type species of *Carteriospongia* Hyatt by subsequent designation of Burton (1954), has abundant foreign material incorporated into the dermis and the primary fibres. *Spongia papyracea* Esper, the type species of *Phyllospongia* Ehlers, is understood by Burton to have no sandy inclusions in either the fibres or the cortex. Ehlers (1870) does not comment specifically on this feature. Many authors (Dendy, Ridley, Bowerbank, de Laubenfels) have described sponges with cored ascending fibres as *P. papyracea*. De Laubenfels (1948) suggests that the type specimen is one in which primary fibres are rare or absent and that the specimens described by later authors are congeneric with Esper's sponge even though they possess varying amounts of debris in both cortex and primary fibres. The commonly accepted view of *Phyllospongia* is of a sponge with a variable amount of debris in both fibres and cortex, and in keeping with this view the Palau specimens are assigned to *Phyllospongia*. A restudy of *Spongia papyracea* Esper is required to clarify this problem.

**DISTRIBUTION:** Red Sea, Indian Ocean, Malaya, Australia, New Zealand,<sup>3</sup> West Central Pacific.

*Phyllospongia dendyi* Lendenfeld

Fig. 4a, b

*Phyllospongia dendyi* Lendenfeld, 1889, p. 177, pl. 14, fig. 5.

*Phyllospongia dendyi* var. *frondosa* Lendenfeld, 1889, p. 178, pl. 14, fig. 5.

*Phyllospongia dendyi* var. *digitata* Lendenfeld, 1889, p. 178.

*Phyllospongia dendyi* Burton, 1934, p. 573.

**OCCURRENCE:** Sta. 92.

**DESCRIPTION:** This sponge consists of somewhat inclined lamellae decreasing in height from the center to the margin and often bearing lobe-like secondary lamellae on the outer surface. The lamellae arise from a spreading base and tend to intersect to form a series of pouches. The free margins of the lamellae are undulat-

<sup>3</sup> This record is doubtful; Lendenfeld described several species and varieties of *Phyllospongia* from New Zealand, none of which has been verified.

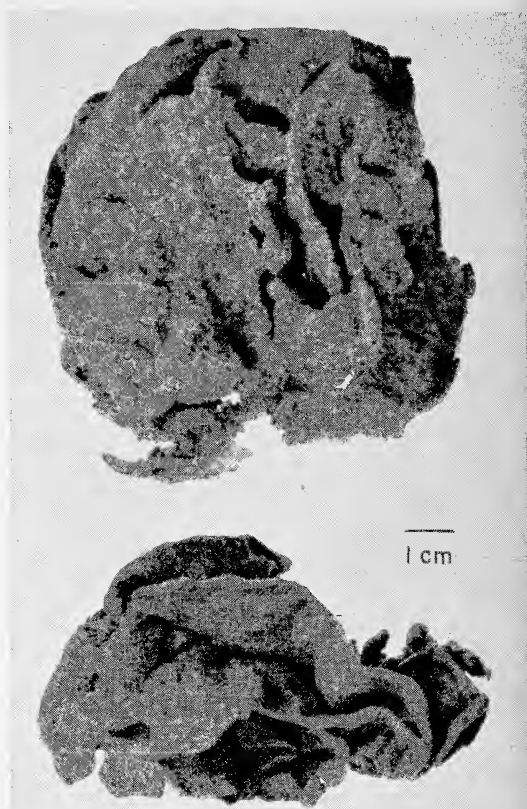


FIG. 4a. Lower, *Phyllospongia dendyi* Lendenfeld. Sta. 92. Upper, *Fasciospongia chondrodes* (de Laubenfels). Sta. 92A.

ing, particularly the outer series. The single specimen is 10 cm long, 5.0 cm wide and 6.0 cm high; lamellae are 2.0–3.2 mm thick.

**COLOR:** In alcohol, dark reddish-brown, between (rY-R 5/2) and (rY-R 5/3).

**TEXTURE:** Fleshy but sufficiently elastic for the sponge to regain its shape after being compressed.

**SURFACE:** Covered evenly with sharp fine conules up to 0.5 mm high. Oscules are scattered over the sides of the lamellae and range from 0.2–1.2 mm in diameter. Narrow subdermal channels are visible through the dermal membrane; these meander over the surface in certain areas and are absent near the edges of the lamellae.

**SKELETON:** Composed of primary fibres cored with spicule fragments and running diagonally through the lamellae. They are connected by a network of uncored secondary fibres.

Primary fibres are  $63\text{--}100\mu$  in diameter; secondaries,  $10\text{--}32\mu$ . No cortex of foreign material is developed over either surface of the lamellae, but numerous spicule fragments occur throughout the body of the sponge and in patches on the surface. The major part of the surface is clear of debris.

**CORTEX:** A collenchymatous layer of variable thickness, rich in spongin A and containing many dark-staining cells with dendritic processes. The thickness of the cortex is comparable on both surfaces of the lamellae varying from  $62\text{--}187\mu$ .

**ENDOSOME:** A remarkable feature of the endosome is the presence of quantities of a blue-green alga filling all available space between flagellate chambers and canals. Flagellate chambers are slightly oval and are large for the Spongiidae,  $37\text{--}65 \times 32\text{--}42\mu$  ( $36 \times 47\mu$ ). De Laubenfels (1948) mentions in connection with the genus *Thorecta* that large flagellate chambers are common; Poléjaeff has described large flagellate chambers in his *Phyllospongia radiata*. I have found the chambers of *P. foliascens* and *Fasciospongia chondrodes* from the Palau Islands to be in excess of  $40\mu$ . In view of the frequency with which large flagellate

chambers occur in sponges which undoubtedly belong to the Spongiidae, it is suggested that this feature should not be used to distinguish between the Spongiidae and the Dysideidae. Emphasis should be laid on the structure of the chamber system rather than on the absolute dimensions of individual units.

**DISCUSSION:** No good description of *Phyllospongia dendyi* is available. Lendenfeld's descriptions were based on dry specimens and Burton (1934) did not give any morphological details. There are several important differences between the Palau specimens and Lendenfeld's description: (1) the Palau specimens lack fasciculate primary columns and special dermal fibres; (2) the primary fibres are up to  $120\mu$  wide in the Australian specimens,  $99\mu$  in the Palau specimen. Despite these differences, the habit of this sponge is distinctive and the broad features of its morphology are comparable with *P. dendyi*. On this basis the Palau sponge is referred to this species. De Laubenfels (1948) has referred *P. dendyi* to *P. papyracea* var. *macropora*. This view cannot be supported from Lendenfeld's descriptions. It is useful to retain this species until a restudy of type material can confirm the identification.

**DISTRIBUTION:** Australia (Lendenfeld, Burton).

#### GENUS *Fasciospongia* Burton

##### *Fasciospongia chondrodes* (de Laubenfels)

Figs. 4a, 5a, b

*Spongionella chondrodes* de Laubenfels, 1954, p. 26, fig. 13.

**OCCURRENCE:** Sta. 92, 92A.

**DESCRIPTION:** The type description (de Laubenfels, 1954) was based upon a fragment of a specimen distorted by the presence of numerous embryos and is therefore misleading in many details.

The sponge grows as a series of interconnected lamellae from a thin spreading basal plate. From both surfaces of the erect plates subsidiary phalanges arise sometimes forming small pouches, in other cases merely forming prominent ridges. There are three sponges described from the Palaus which have this dis-



FIG. 4b. *Phyllospongia dendyi* Lendenfeld. Portion of the fibre network at right angles to the surface.

tinctive habit, *Fasciospongia chondrodes*, *Dysidea herbacea*, and *Phyllospongia dendyi*.

COLOR: In alcohol, varies from pale pinkish-purple (RY-R 6/2), to yellowish-gray (rY 7/4), to pale creamy (rY 8/4), in the holotype.

TEXTURE: Stiff and rather cartilaginous.

SURFACE: In the holotype, almost smooth; in the other two specimens it is irregularly conulose in such a way as to give an over-all spined appearance and to render the edges of all lamellae crenulate. Some parts of the sponge are almost smooth where the dermal membrane is stretched between adjacent ridges. Conules are simple or multiple; sometimes the primary fibres are produced beyond the surface. A system of tangential dermal fibres is developed, being plainly visible in the Palau material and just discernible in the holotype. The dermal membrane is granular and skinlike and is not easily separable from the underlying cartilaginous cortex, the two layers together being 200–250 $\mu$  thick.

SKELETON: Composed of a compact reticulation of secondary fibres from which the primary fasciculated columns rise abruptly and extend through the collagenous cortex into the conules. All fibres are finely laminated and a pith is present, distributed sporadically in both primary and secondary fibres. Only the primary columns are cored by spicule fragments. There is no sand cortex.

The primary fibres range from 70–180 $\mu$  in diameter; the secondaries, from 25–160 $\mu$ .

De Laubenfels stated that there were no cored fibres in the type of *Spongionella chondrodes*, but this is an error. All primary fibres are fascicular, pithed, and cored with spicule fragments.

CORTEX: A dense layer, 180–800 $\mu$  deep, usually 250 $\mu$ , rich in spongin A. It contains abundant dendritic cells with granular cytoplasm which are possibly pigment-containing cells. A specimen of *Fasciospongia cavernosa* (Schmidt) from Marseilles has been examined

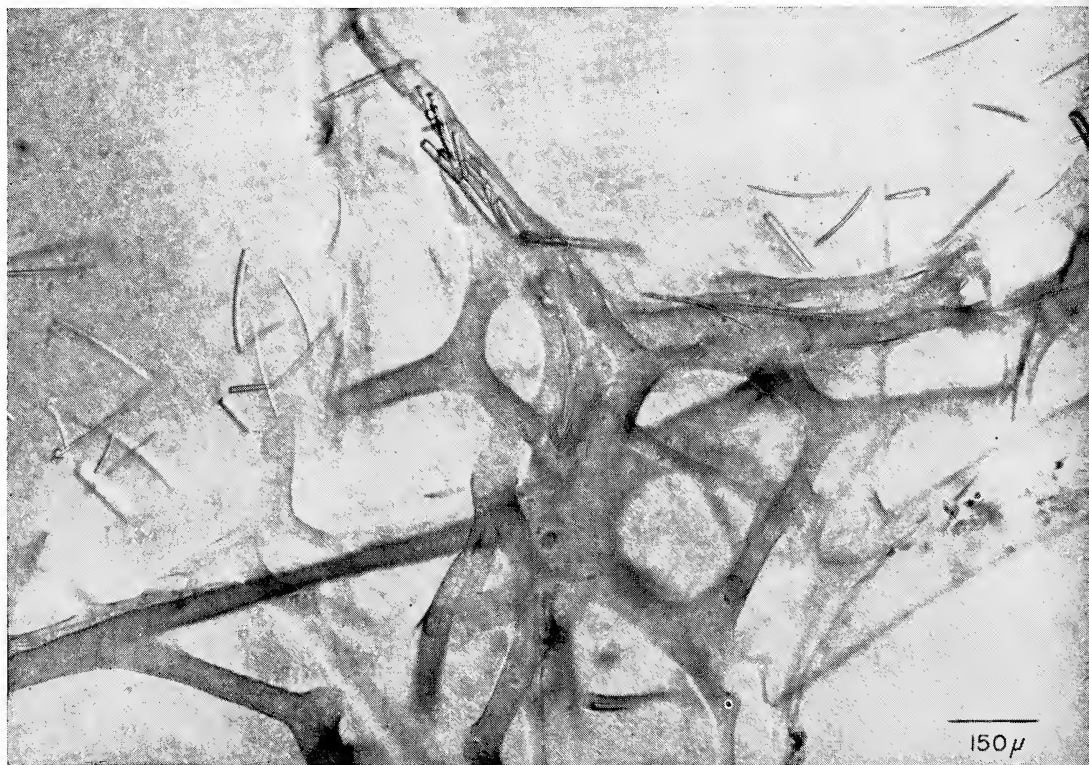


FIG. 5a. *Fasciospongia chondrodes* (de Laubenfels). Sta. 92. Section at right angles to the surface showing the fasciculate fibre system, the coring spicules in the ascending fibres, and (lower left) traces of pith and concentric lamination in the fibres.

and also has a dense collagenous cortex. The same feature is characteristic of the type species, *Fasciospongia fovea* (Lendenfeld), from Australia.

**ENDOSOME:** Cavernous and contains a dense, irregular network of fibres. Flagellate chambers tend to be localized, groups of chambers being separated by areas of collagenous tissue. Considerable variation in size and shape characterizes the chambers. They are somewhat oval in two specimens,  $19.8 \times 16.5\mu$  to  $30 \times 22\mu$  and  $37 \times 23\mu$  to  $50 \times 44\mu$  spherical,  $26\text{--}49\mu$ , in the other.

Vacelet (1959) commented upon the chamber size of *Spongionella chondrodes*, recorded as  $25\text{--}30\mu$  by de Laubenfels, and concluded that this sponge did not belong in *Spongionella*. It is noteworthy that the type specimen of *S. chondrodes* has much larger chambers than de Laubenfels states and that they tend to be oval, but not eurypylous. It is impossible, however, to be sure that the above dimensions are accurate, for the chambers in almost all cases are not lying *in situ*. The collagenous ground substance in which they lie has contracted, leaving the groups of flagellate cells lying in spaces in the matrix. The two Palau specimens are in good condition and perhaps reflect more reliably the structure of this species.

**DISCUSSION:** A restudy of the holotype (USNM 23112) and the paratype (Bishop Museum 153) of *S. chondrodes* in conjunction with the two specimens included in this collection leaves little doubt that this sponge is a *Fasciospongia*. More information on the nature of the flagellate chambers in other species of *Fasciospongia* would be desirable, but unfortunately the type of *F. fovea* (Lendenfeld) cannot be located at present. It seems that variation in size and shape of the chambers in *F. chondrodes* is greater than is usual in the Spongiidae. In my specimen of *F. cavernosa* the chambers are often slightly oval, measuring  $37 \times 30\mu$ .

**DISTRIBUTION:** Palau Islands.

#### GENUS *Psammaplysilla* Keller

*Psammaplysilla purpurea* (Carter)

Fig. 6a, b, c, d

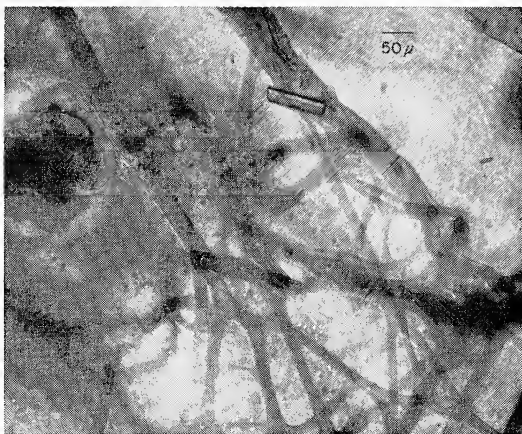


FIG. 5b. *Fasciospongia chondrodes* (de Laubenfels). Holotype, USNM 23112. Section showing fibre reticulum and an embryo.

*Aplysina purpurea* Carter, 1880, p. 36.

*Aplysina purpurea* Carter, 1881, p. 103, pl. IX, fig. 1, a-i, fig. 2, a-c.

*Aplysina purpurea* Dendy, 1889, p. 97.

*Psammaplysilla arabica* Keller, 1889, p. 358, pl. XXII, figs. 23-27.

*Psammopemma fuliginosum* Lendenfeld, 1889, pars. p. 636.

*Druinella ramosa* Thiele, 1899, p. 24, pl. 3, fig. 3, pl. 4, fig. 5.

*Aplysina purpurea* Dendy, 1905, p. 224.

*Aplysina purpurea* Row, 1911, p. 377.

*Aplysina purpurea* Hentschel, 1912, p. 437.

*Psammaplysilla kelleri* Wilson, 1925, p. 488, pl. 44, fig. 3.

*Druinella purpurea* Burton, 1934, p. 594.

non *Druinella ramosa* Burton, 1934, p. 595.

*Aplysina purpurea* Brøndsted, 1934, p. 26.

*Cacospongia ramosa* pars. de Laubenfels, 1948, p. 95.

*Hexadella pleochromata* de Laubenfels, 1950, p. 10.

*Thorectopsamma xana* de Laubenfels, 1954, p. 32, fig. 16.

*Dendrilla verongiformis* de Laubenfels, 1954, p. 45, fig. 25.

*Druinella tyroensis* de Laubenfels, 1954, p. 27, fig. 14.

non *Druinella ramosa* Burton, 1959, p. 269.

non *Psammaplysilla arabica* Burton, 1959, p. 271.



OCCURRENCE: Sta. 12, 60, 92, 100, 134.

DESCRIPTION: The six Palau specimens of this sponge range in habit from thin encrustations (Sta. 134) to massive with a single stout branch (Sta. 12), or are ramose (Sta. 12, 60, 92, 100) and repent. The branches of the ramose specimens anastomose frequently. In two cases the branches arise from a massive, spreading portion which incorporates much shell and sand (see also de Laubenfels, 1954: 33).

DIMENSIONS: The encrusting specimen is 0.8–1.0 mm thick, covering an area 6.5 cm ×

4.5 cm on the under surface of a *Fungia*. The ramose specimens have almost cylindrical branches which are up to 28 cm long and from 0.5–2.0 cm wide.

COLOR: In alcohol, dark reddish-brown both internally and externally; the exact shade varies with each specimen from (RY-R 2/2–RY-R 3/6–YR3/2–rY-R 2/2). In one specimen (Sta. 12) the tips of the branches, both inside and out are light pinkish-red (rY-R 5/2). The color in life is described as bright green; de Laubenfels has recorded it as yellow (in *Thorectopsamma xana*) and yellow tinged with green (in *Dendrilla verongiformis*).



FIG. 6a. *Psammaplysilla purpurea* (Carter). Upper left, Sta. 12; upper right, Sta. 92. Center left, *Dendrilla verongiformis* de Laubenfels, holotype. Lower left, Sta. 92; lower center, *Thorectopsamma xana* de Laubenfels, holotype; lower right, Sta. 12.

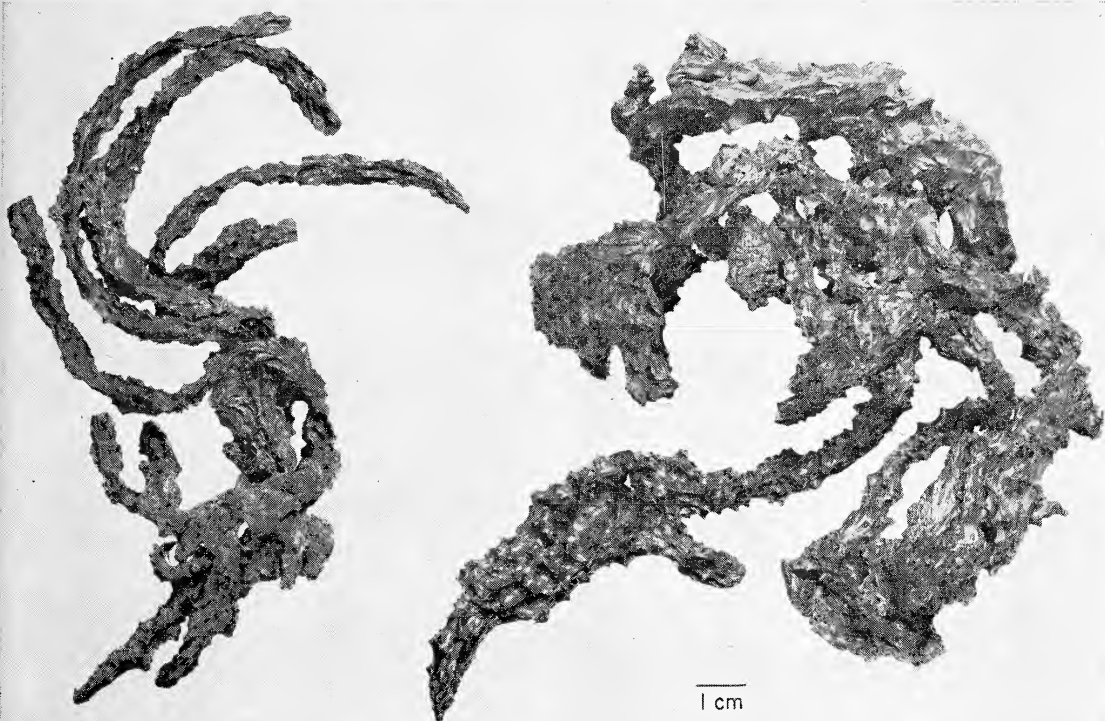


FIG. 6b. *Psammaphysilla purpurea* (Carter). Left, *Psammaphysilla kelleri* Wilson, holotype. Right, Sta. 60. USNM 23708.

**TEXTURE:** Firm, rather elastic in some cases, stiffer in others.

**SURFACE:** Always conulose, but the height and spacing of the conules differ with the specimen from few, low, rather rounded projections in the thinly encrusting specimen to blunt, tall, and abundant in the specimens from Sta. 60. In most specimens, conspicuous ridges connect adjacent conules. The dermis is thick, smooth, and with no apparent pores. Oscules are irregularly dispersed, oval and 2.5–7.0 mm in longest dimension.

The surface of the holotype of *Druinella tyroëis* is conspicuously reticulated between the ridges diverging from the conules. This type of structure was described by Carter (1881) for *A. purpurea*, but is not well shown in any of the Palau specimens.

**SKELETON:** A reticulation of irregular, concentrically stratified fibres which are themselves built up as a reticulum of extremely fine threads. In many places irregular lobes arise from the

fibres. Most authors have given recognizable descriptions of the skeleton of this species, none better than Keller (1889) and Wilson (1925). Inclusions in the form of sand grains vary in quantity from specimen to specimen. Some lack them entirely. Spicule fragments occur sporadically. There is a tendency toward the fusion of fibres at the base of the sponge, giving the appearance of a basal plate; this is, however, not well marked in most specimens. The fibres of this sponge are composed entirely of the reticulate substance which makes up the pith in other verongioid genera. The concentric structure is often more compact at the surface and gives the impression of an outer, more dense layer. The extreme irregularity of the fibres makes measurements of little value, but those quoted by Wilson (1925) are typical.

**CORTEX:** Of variable thickness and composed of dense spongin A, broken into patches by the numerous pore canals. In specimens where the branches are wider the endosome has a more

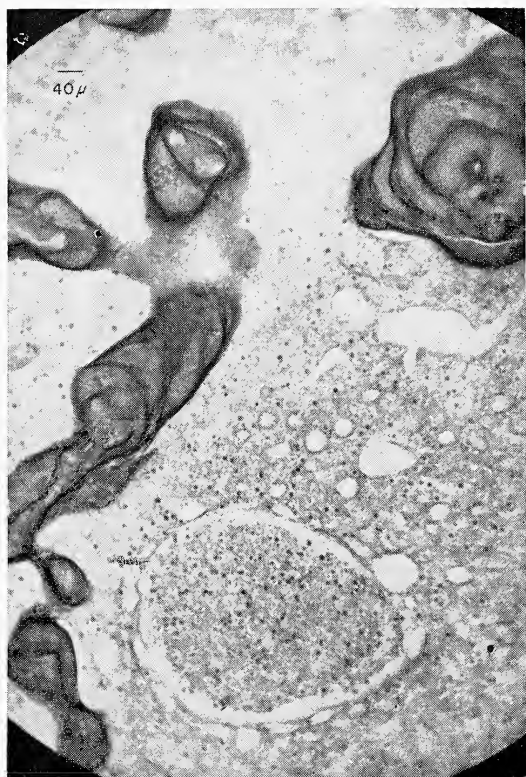


FIG. 6c. *Psammaplysilla purpurea* (Carter). Photomicrograph showing branching of fibres and structure of the flagellate chambers. One of the ellipsoid masses of dense tissue of unknown function is shown at lower center.

open structure and the cortical region is narrow (75–100 $\mu$ ) [e.g., Sta. 60; *Dendrilla verongi-formis* USNM 23104; *Druinella purpurea* (Burton, 1934)]. In those specimens where the over-all texture is tough and the branches are thinner, the cortex may be up to 350 $\mu$  thick [e.g., *Thorectopsamma xana* USNM 22994; *Psammaplysilla kelleri* USNM 21241; specimen from Sta. 92].

**ENDOSOME:** Earlier workers (Lendenfeld, 1889; de Laubenfels, 1954) have mentioned that the flagellate chambers tend to be concentrated around the excurrent canals and are lacking from large areas of the sponge. After examining several specimens, including the sponges which de Laubenfels described, it is apparent that this is not strictly the case. Chambers are aggregated around the excurrent canals but in all specimens groups of chambers are

more or less evenly dispersed throughout the endosome. In compact specimens (such as the type of *D. tyroensis*) the relatively great extent of the cortex gives the impression that the chambers are restricted in occurrence. The structure of the flagellate chambers is in no way remarkable. They do not have long fine prosodal canals, but long aphodal canals do occur and vary in length (up to 100 $\mu$ ) and diameter from specimen to specimen. The chambers themselves are small and slightly ellipsoidal, 23  $\times$  12 to 46  $\times$  30 $\mu$ . A constant feature of the species is the occurrence throughout the endosome of ellipsoidal masses of relatively deep-staining cells. These are figured by Wilson (1925: pl. 44) but no comment is offered as to their possible function. They are always set off from the surrounding mesenchyme by a concentrated zone of spongin A which often extends inward as bands between the cells. It is possible that these structures represent developmental stages of the fibres.

**DISCUSSION:** In order to elucidate the systematic affinities of *Psammaplysilla purpurea* (Carter) it was necessary to investigate the sponges assigned to the genus *Druinella* Lendenfeld for, superficially at least, the two genera are closely similar.

Lendenfeld (1889) described *Druinella* to receive *D. rotunda* from Australia. This sponge was notable for the lobose knotty fibres and for the possession of long prosodal and aphodal canals. In all features except the possession of these canals, *D. rotunda* is inseparable from *Aplysina purpurea* Carter. Burton (1934) was the first worker to definitely associate *Aplysina purpurea* Carter with the genus *Druinella*. Wilson (1925) had tentatively suggested that *Psammaplysilla kelleri* and *P. arabica* belong to the same genus as *A. purpurea*, and likened all of these species to *Druinella* and *Thymosia* (Topsent).

No author since Lendenfeld's time has seen *Druinella rotunda* nor had similar canal structure been described from any other sponge<sup>4</sup> until de Laubenfels (1948) referred *Cacospongia camera* de Laubenfels to *Druinella*. He

<sup>4</sup> A similar pattern of short canals is well known from the work of Schulze (1878) on the Aplysinidae.



claimed to have observed just such a chamber structure as Lendenfeld figured for *Druinella rotunda*. Examination of the type, and only, specimen of *C. camera* (USNM 22405) shows it to be a poorly preserved sponge containing quantities of filamentous blue-green algae and having normal spongin fibres. The cell structure of the sponge is largely dissociated. Those traces of flagellate chambers which remain indicate that the chambers were quite large (40–60 $\mu$ ) and possibly eurypylous. *Cacospongia camera* does not belong in *Druinella*, and should be pronounced unrecognizable.

Thiele (1899) identified a sponge from the Celebes as *Druinella ramosa*. He stated that he had not been able to study the flagellate chambers and that the identification was based on similarity of habit and fibre structure. Burton (1934, 1959) has referred sponges to *D. ramosa*; preparations of both of these have been examined and clearly neither belongs to *Druinella*. The two sponges belong to different genera. One (BM 1930.8.13.201) is possibly a *Dactylospongia* but certainly belongs to the Spongiidae; the other (BM 1930.3.4.155) is probably a *Cacospongia*, but the fragments examined were too small to allow further identification.

Only one other sponge has been described in the genus *Druinella*, namely *tyroensis* de Laubenfels. This sponge is identical with the specimens of *Psammaphysilla purpurea* from Palau except that it is more compact; the endosome is extremely compressed and full of Spongin A and the aphodal canals show clearly. No structure comparable with that described for *D. rotunda* can be found in the holotype (USNM 23052).

Burton (1934) referred *Aplysina purpurea* Carter to *Druinella* as *Druinella purpurea* and, presuming Carter's original specimen to be lost, named Dendy's specimen from the Gulf of Manaar as neotype. The reasons for referring this sponge to *Druinella* rather than *Psammaphysilla* were not given but were certainly not based on histological study of *Druinella rotunda*. In the text of the same work Burton refers *Aplysina purpurea* Carter (1881) from Ceylon and Australia to *Psammaphysilla* in contradiction to his reference in the synonymy, where it is placed in *Druinella purpurea*. Bur-

ton differentiates Carter's later specimens (1881) from the type specimen (Carter, 1880) and that described by Dendy (1905) by stressing the fasciculate fibre network in the former, a structure identical to that figured by Keller (1889) for *Psammaphysilla arabica*. There is nothing in Carter's original description or in Dendy's account of his specimen to give basis to the assumption that such a skeletal structure is absent. On the contrary, all accounts of the skeleton of this sponge agree remarkably, and Dendy specifically describes "compound fibres."

The type specimen of *Druinella rotunda* has been lost; it is not at the British Museum; the Australian Museum, Sydney; or the National Museum of Victoria, Melbourne. Since, first, the only specimen of the type species (*D. rotunda*) is lost; second, the type description is poor and could easily refer to *Psammaphysilla purpurea*; and third, all subsequent records of *Druinella* are referable to *Psammaphysilla*, it is suggested that the genus *Druinella* be considered unrecognizable and that the genus *Psam-*

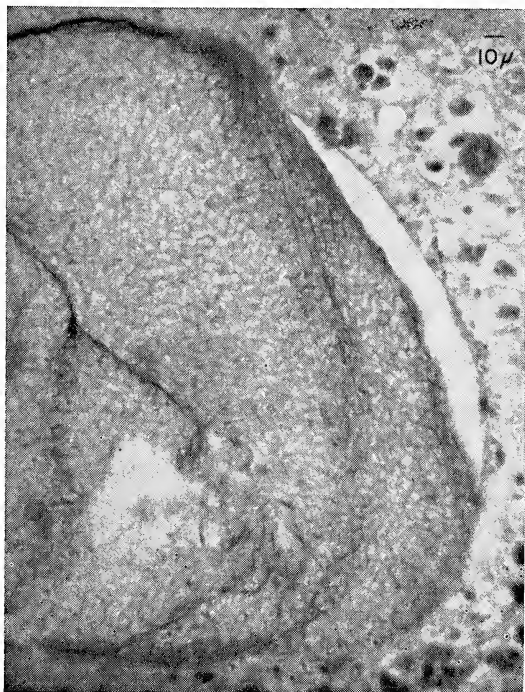


FIG. 6d. *Psammaphysilla purpurea* (Carter). Photomicrograph showing the reticulate structure of the fibres.

*maplysilla* Keller be used for *Aplysina purpurea* Carter and its synonyms.

*Psammaplysilla arabica* was well described by Keller (1889) except for the canal system, and there can be little doubt that it is the same sponge as *A. purpurea* Carter. Certainly the two belong in the same genus, the affinities of which are with genera such as *Verongia* rather than with the Aplysillids (Dendy, 1905).

No significant difference can be found in the descriptions of *Psammaplysilla arabica* and *Psammaplysilla kelleri* Wilson. The type of the latter (USNM 21241) has been examined and its identity with the Palau specimens established. *P. kelleri* is from the Celebes, as is *Druinella ramosa* Thiele, and these are considered identical. *Druinella purpurea* (Burton, 1934, BM 1930.8.13.197) has also been examined and is identical with the above. Row (1911) considered that *P. arabica* and *A. purpurea* may belong to the same species, but he appended a query to his synonymy. Burton has not endorsed the synonymy and in 1959 recorded a specimen of *P. arabica* (BM 1936.3.4.574) from Suakin. This sponge has been examined and, while no opinion can yet be offered as to what it is, it certainly is not *P. arabica*.

De Laubenfels (1954) described *Thorectopsamma xana* (USNM 22994) and *Dendrilla verongiformis* (USNM 23104) from the Palau. The types and paratypes of these sponges have been examined and all specimens are referable to *P. purpurea*.

*Hexadella pleochromata* de Laubenfels, from Hawaii (USNM 22748) is an encrusting specimen of *P. purpurea*, and closely resembles the holotype of *Druinella tyroensis*.

All of the species listed in the synonymy above are identical in their possession of a unique type of fibre and in their color. Many of the early specimens were either dry or poorly preserved and thus, until the work of Wilson (1925), no reliable description of the flagellate chambers was available. In Wilson's specimen it is difficult to see the chambers because of the density of the spongin. A. Burton (1934) commented that too much emphasis on color and too little attention to the more important details of histology has led to confusion in this complex. This statement is perhaps true, but it

appears from the literature that, with the possible exception of Lendenfeld, no author up to the time Burton made the statement had satisfactory material for histological study. Burton, however, did not publish the desired histological details. De Laubenfels collected his own material, which is in an excellent state of preservation, but only in the small semiencrusting fragment described as *Druinella tyroensis* did he observe aphodal canals.

DISTRIBUTION: Gulf of Manaar (Carter, Dendy); Ceylon (Carter); S. W. Australia (Carter); Red Sea (Keller, Row); Celebes (Thiele, Wilson); Gt. Barrier Reef (Burton); East Indies (Brøndsted); Caroline Islands, Marshall Islands, Palau Islands, Hawaii (de Laubenfels).

#### FAMILY DYSIDEIDAE Gray

#### GENUS *Dysidea* Johnston

#### *Dysidea herbacea* (Keller)

Fig. 7a, b, c

#### RESTRICTED SYNONYMY:

*Spongelia herbacea* Keller, 1889, p. 336, pl. 20, fig. 1.

*Dysideopsis palmata* Topsent, 1897, p. 482, pl. XX, fig. 25.

*Spongelia delicatula* Row, 1911, p. 364.

*Phyllospongia cordifolia* Row, 1911, p. 378.

*Dysideopsis topsentii* Hentschel, 1912, p. 439.

*Dysidea herbacea* Burton, 1934, p. 593.

*Phyllospongia complex* de Laubenfels, 1954, p. 18, fig. 8, pl. 3, fig. 6.

non *Dysidea herbacea* de Laubenfels, 1954, p. 38.

OCCURRENCE: Sta. 10, 60.

DESCRIPTION: The habit of the sponge is well described and figured by de Laubenfels (1954: pl. III, fig. 6). Beyond this point, however, his description is completely unrelated to *Dysidea herbacea*. The following description is based upon the holotype (USNM 23110) and paratypes (USNM 23127 and Bishop Museum 148) of *Phyllospongia complex* de Laubenfels and two additional specimens from our Palau collections.

COLOR: In life, gray; in alcohol, yellowish-gray (between Y-R-Y 7/2 and rY 7/4) to



FIG. 7a. *Dysidea herbacea* (Keller). Lower left and right, Sta. 10; upper center, specimen from Tonga showing surface characteristics intermediate between Palau Is. specimens of *D. herbacea* and *D. chlorea*.

purplish pink (yR 4/2) in the specimen from Sta. 60. The color in life appears to vary from gray to greenish depending upon the amount of algae in the sponge tissue.

**TEXTURE:** Resembles that of soft leather. One specimen (Sta. 60) is tough and rigid; this sponge contains more and coarser detritus than any other examined.

**SURFACE:** Finely conulose; individual conules range up to 0.4 mm high, with a tendency to be aligned in vertical rows which give an over-all slightly striated appearance to the sponge surface. This feature is most noticeable in the specimen from Sta. 10, but is discernible in patches on all specimens.

**SKELETON:** An open network of fibres cored with sand grains of extremely irregular dimensions. There is no distinction between primary

and secondary fibres; the range in diameter is  $50\text{--}153\mu$ . A layer of foreign material is present on both surfaces,  $27\text{--}90\mu$  deep and essentially contained within the dermal membrane, only rarely extending into the cortical region. In the specimen from Sta. 60, inclusions in the fibres are coarser and more irregular and here the superficial debris often extends into the body of the sponge.

**ENDOSOME:** The skeleton is loose and the cortex relatively thin; consequently most of the thickness of the lamellae is endosome. Flagellate chambers are abundant, oval,  $54\text{--}120 \times 28\text{--}82\mu$  and eurypylous; the collagenous endosomal matrix surrounding them is packed with blue-green algae.

**DISCUSSION:** All specimens making up the type series of *Phyllospongia complex* de Lau-



FIG. 7b. *Dysidea herbacea* (Keller). Sta. 60.

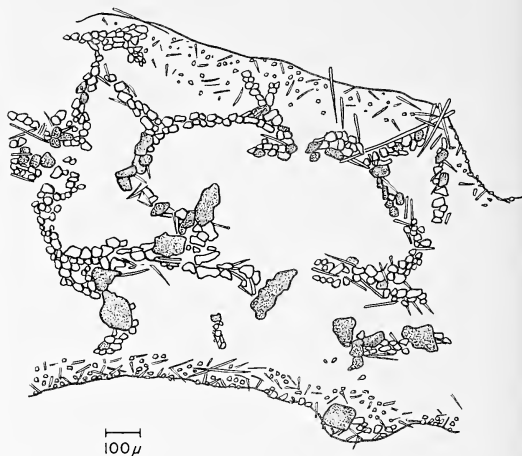


FIG. 7c. *Dysidea herbacea* (Keller). Cross section of lamella to show the disposition of fibres and surface detritus.

benfels belong to the genus *Dysidea*. Many features of the type description (de Laubenfels, 1954:18) however, are inconsistent with this generic identification. This can possibly be explained if one assumes that among his specimens, which are here correctly assigned to *Dysidea herbacea*, de Laubenfels collected a fragment at least of *Phyllospongia dendyi* and subsequently sectioned and described this and not the *Dysidea*. The growth form of these two sponges is similar, and they occur in the same locality.

Burton (1934) lists several synonyms of *D. herbacea*, not all of which belong to this species. The holotype of *Spongelia delicatula* Row has been examined and is certainly *D. herbacea*; similarly with Row's specimen assigned to *Phyllospongia cordifolia*. *Spongelia digitata* Sollas bears some resemblance to *D. herbacea* but cannot certainly be referred here. De Laubenfels' Pacific specimens labelled *D. herbacea* belong to a new species, *Dysidea granulosa*.

**DISTRIBUTION:** Red Sea (Keller, Row, Top-sent); Indian Ocean (Dendy); Australia (Hentschel, Burton); Marshall Islands (de Laubenfels).

*Dysidea chlorea* de Laubenfels

Fig. 8a, b

*Dysidea chlorea* de Laubenfels, 1954, p. 37, fig. 19.

*Dysidea chlorea* de Laubenfels, 1955, p. 138.

**OCCURRENCE:** Sta. 47, 92, 219.

**DESCRIPTION:** In habit the three specimens above agree relatively closely with the type description. They are digitate sponges with projections 2.0–4.0 mm wide rising to a height of 2.5 cm from an apparently encrusting base 1.5 mm thick. In the sponge from Sta. 47 it is difficult to decide what the growth form was, as the specimen has been crushed. It could have been sprawling or even erect, since the projections are developed on both sides of the body, and the body is 3.0 mm thick at one end. The holotype (USNM 22971) consists of two fragments of a sponge that may have been similar to the specimen from Sta. 219 but which had the vertical projections slightly more crowded.

**COLOR:** In alcohol, yellowish brown (Sta. 219) (Y-R-Y 7/4) to dark brick red (yR 4/4) (Sta. 47).

**TEXTURE:** Soft and easily compressible.

**SURFACE:** Conulose with conules 0.3–1.0 mm high distributed at intervals of 1.2–3.5 mm. No oscules or pores are visible.

**SKELETON:** A loose reticulation of exceedingly fine fibres, cored with sand grains and showing little division into ascending and connecting fibres except where a fibre enters a conule. Often the fibre projects up to 400 μ beyond the sponge surface and macroscopically the conules appear to have fine white apical hairs.

The fibres are from  $25\text{--}80\mu$  in diameter. Fragments of sand and spicule debris occur in the dermal membrane on one surface only but form a very thin layer, not a continuous cortex.

**HISTOLOGY:** A dermal membrane  $12\text{--}20\mu$  thick overlies a cortical region of variable thickness. The dermal region is made up of a densely cellular layer with little extracellular matrix; the cells have prominent nuclei and granular cytoplasm. Deep to this layer is a zone in which the concentration of spongin A greatly exceeds that of the cortex; this layer appears to serve as a basement membrane. The cortex contains many granular spindle-shaped cells with prominent nuclei set in a clear ground substance.

The endosome is cavernous and contains large numbers of symbiotic blue-green algae. Flagellate chambers are abundant, large, and eurypylous.

*Dimensions of flagellate chambers.*

Holotype, USNM 22971:  $59\text{--}70 \times 36\text{--}62\mu$

Sta. 47:  $62\text{--}75 \times 37\text{--}48\mu$

Sta. 219:  $55\text{--}75 \times 38\text{--}48\mu$

**DISCUSSION:** The species of *Dysidea* are extremely difficult to define on morphological grounds since, frequently, specimens of fundamentally different habit are identical or closely comparable in internal structure. De Laubenfels

considered it possible that *Dysidea chlorea* was merely a variant of *D. fragilis*.

Much attention has been given to the variability of *D. fragilis* (Burton, 1934; de Laubenfels, 1948), which appears to be a sponge in which the amount and type of debris incorporated in the skeleton can vary within wide limits; detritus is, however, not usually present in the form of a superficial cortex. The presence of such a sand cortex is characteristic of *D. chlorea*. A further difference between the two species is the nature of the fibres, which are extremely fine and regular in all specimens of *D. chlorea*. These features, in conjunction with the peculiar growth form, are sufficient to separate *D. chlorea* and *D. fragilis*.

In *D. herbacea* a complex lamello-digitate habit is coupled with coarse, irregular fibres and a well-defined sandy cortex. Until it is known to what degree these features are relevant in separating the species of *Dysidea*, it is practicable to retain both *D. chlorea* and *D. herbacea*.

**DISTRIBUTION:** Marshall Islands; Hawaii (de Laubenfels).

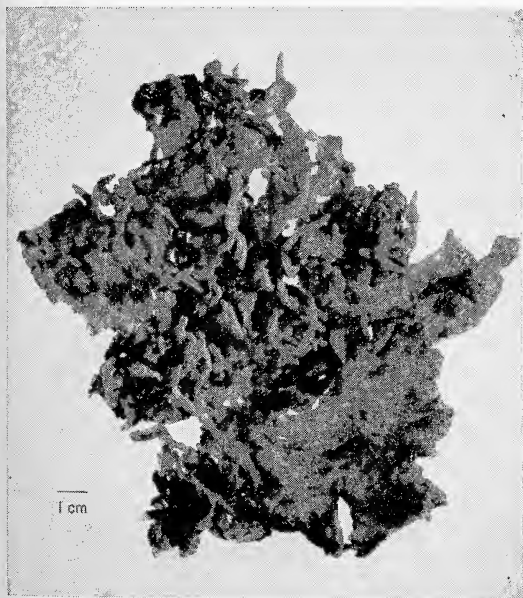


FIG. 8a. *Dysidea chlorea* de Laubenfels. Sta. 219. USNM 23705.

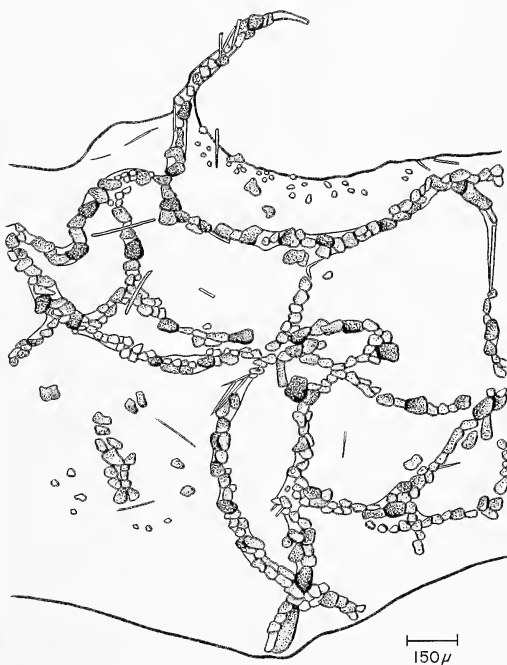


FIG. 8b. *Dysidea chlorea* de Laubenfels. Cross section of the sponge base showing the loose fibre network.

*Dysidea granulosa* n. sp.

Fig. 9

OCCURRENCE: Sta. 61, 125, 220A (holotype).

DESCRIPTION: *Dysidea granulosa* is represented in this collection by three specimens, all of which are thin cylindrical erect sponges growing from a narrow base. One specimen is incipiently branched. The holotype and only complete specimen (Sta. 220A; Fig. 9, left) is 12.5 cm high, 4.0–6.0 mm in diameter.

COLOR: White, in alcohol.

TEXTURE: Varies from stiff and brittle in the specimen most heavily packed with detritus to firm but flexible in the holotype.

SURFACE: Covered with fine conules, and the general appearance is granular. Oscules are scattered at irregular intervals over the surface and are 2.0–3.5 mm in diameter.

SKELETON: There is no distinction between primary and secondary fibres in the skeleton; the whole is a compact reticulation with irreg-

ular meshes. The fibres are uneven, from 50–162 $\mu$  in diameter and cored with sandy detritus. Very little clear spongin remains in the fibres except occasionally where the fibre narrows abruptly and no detritus occurs. The dermal membrane is densely charged with detritus, and this extends inward as a sand cortex up to 80 $\mu$  deep in some places.

ENDOSOME: Flagellate chambers are oval, eurypylous, 54–75  $\times$  40–54 $\mu$ ; the tissue surrounding the chambers in one specimen is packed with filamentous blue-green algae.

DISCUSSION: This sponge can be differentiated from other species of *Dysidea* by its consistently simple fingerlike habit in conjunction with fine evenly distributed surface conules. In other features, such as the absence of any distinction between primary and secondary fibres and the presence of a sandy cortex, *D. granulosa* can be compared with *D. herbacea* and *D. arenaria*. However, these three species are sharply distinct in habit.

The difficulty of fixing on morphological characters to separate species of *Dysidea* has been mentioned above. In all cases dealt with here growth form and habit seem to be the most reliable characters. De Laubenfels' (1954) specimens assigned to *Dysidea herbacea* properly belong in *D. granulosa*.

*Dysidea arenaria* n. sp.

Fig. 10a, b

OCCURRENCE: Sta. 125 (Holotype, USNM 23698).

DESCRIPTION: A single specimen of this sponge is in the Palau collection and this is designated as holotype. The sponge is irregularly ramose, 9.0 cm high, 10 cm wide, with frequent anastomoses between the branches. Individual branches are 3.0–7.0 cm high, 0.9–3.5 cm thick, rising from a narrow base of attachment.

COLOR: In alcohol, grayish-white (close to M.P., Pl. 36 A/1).

TEXTURE: Stiff, just compressible, and brittle owing to the large quantities of incorporated debris.

SURFACE: Extremely irregular, coarsely conulose, and deeply pitted between conules. The

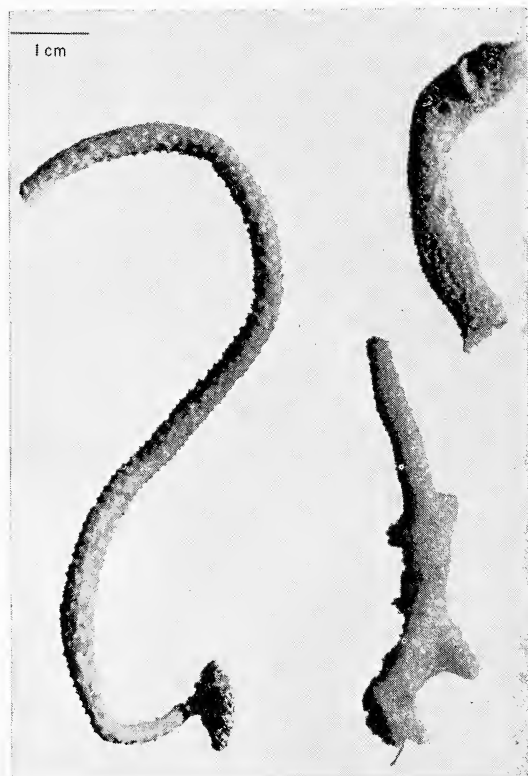


FIG. 9. *Dysidea granulosa* n. sp. Left, Sta. 125; upper right, Sta. 61; lower right, Sta. 220A. Holotype.



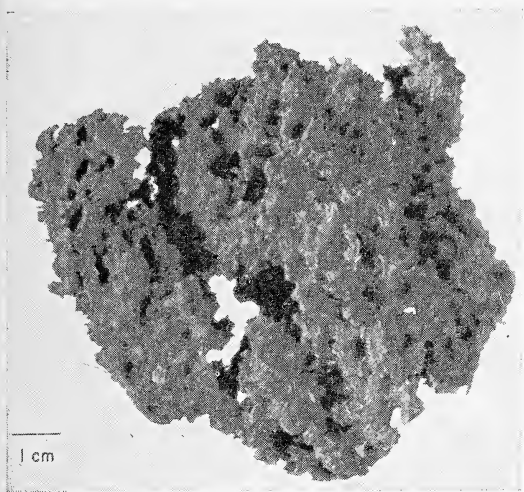


FIG. 10a. *Dysidea arenaria* n. sp. Holotype. USNM 23698. Sta. 125.

conules are often multiple structures, 1.0–5.0 mm high and 20–50 mm apart, receiving as many as four fibres. A prominent tracery of subdermal fibres shows through the dermal membrane, which is packed with sandy detritus.

**SKELETON:** Fibres range from 70–120 $\mu$  in diameter and are not clearly distinguishable into primary and secondary. They are arranged in a reticulate pattern, the meshes of which are compact near the periphery, open toward the center. Where several fibres converge into a conule it is sometimes possible to describe one as “primary.” All fibres are cored with detritus and little clear spongin remains.

**ECTOSOME:** A thick sand cortex, 85–100 $\mu$  deep, is present over the entire sponge.

**ENDOSOME:** The endosome contains large quantities of extra-fibrillar debris, thus rendering study of the soft tissues extremely difficult. Flagellate chambers are oval, 60–85  $\times$  45–60 $\mu$ , and eurypylous.

**DISCUSSION:** This sponge has several features in common with *Dysidea granulosa*: the ramose form, the lack of distinction between primary and secondary fibres, and the presence of a distinct sand cortex. The large and irregular surface conules, the complexity of branching, the incorporation of great quantities of debris in the endosome, and the prominent tracery of sub-

dermal fibres give this sponge a very different appearance from *D. granulosa* from the same locality. *D. arenaria* cannot be confused with *D. fragilis*, as it possesses a sand cortex and lacks distinct primary and secondary fibres.

GENUS *Euryspongia* Row

*Euryspongia lobata* n. sp.

Fig. 11a, b

**OCCURRENCE:** Sta. 100, 220 (Holotype, USNM 23710).

**DESCRIPTION:** This species is erect, lobate to digitate.

**DIMENSIONS (in cm):**

	Height	Length	Width
Sta. 100	5.5	3.5	1.3
Sta. 220	8.0	9.0	2.8

**COLOR:** In alcohol, gray (Sta. 220) near (Y-R-Y 7/2), or reddish-brown (Sta. 100) between (RY-R 4/2) and (RY-R 4/4).

**TEXTURE:** Extremely soft and fleshy, slightly elastic.



FIG. 10b. *Dysidea arenaria* n. sp. Portion of the skeleton drawn at right angles to the surface. At this point primary and secondary fibres can be distinguished; in the interior of the sponge this distinction is lost.



FIG. 11a. *Euryspongia lobata* n. sp. Holotype. USNM 23710. Sta. 220.

**SURFACE:** Coarsely conulose, with sandy detritus arranged in close-set lines diverging from each conule.

	Conule Height (mm)	Conule Spacing (mm)	Oscules (mm)
Sta. 100	1.5-4.0	1.0-5.0	1.0-2.0 lateral
Sta. 220 (Type)	1.0-3.5	1.0-5.5	1.5-3.0 lateral

In the interconular areas the pattern of the surface detritus becomes netlike.

**SKELETON:** In features of the skeleton this species is somewhat intermediate between *Dysidea* and *Euryspongia*.

The primary fibres are cored with spicule debris and are slightly fasciculated. Secondary fibres arise more or less at right angles, are much branched forming rounded meshes, and often include spicule fragments. These never form a continuous core and are not a constant feature of the secondary fibres. The spongin shows no sign of concentric lamination.

Primary fibres are 86-125 $\mu$  (108 $\mu$ ) in diameter, secondaries are 37-57 $\mu$  (42 $\mu$ ).

**ECTOSOME:** The thin dermal membrane contains abundant sandy debris which does not extend into the cortical region. The latter is a compact layer, 30-60 $\mu$  deep, of collagenous tissue containing isolated branched cells and abundant symbiotic blue-green algae.

**ENDOSOME:** Flagellate chambers are abundant, large, oval, and eurypylous, 75-90 $\mu$   $\times$  50-62 $\mu$ . Collagenous tissue containing spindle-shaped cells and algae surrounds the groups of chambers and lines the large canals.

**DISCUSSION:** Coring material extends into the secondary fibres of this sponge and in this regard it resembles a *Dysidea*. In all other features, however, it is more typical of *Euryspongia*.

*Euryspongia lobata* is not particularly close to any other species described thus far in this genus. The surface conules are larger, the primary fibres finer and slightly fasciculate, the fibre reticulation more compact. Except for its

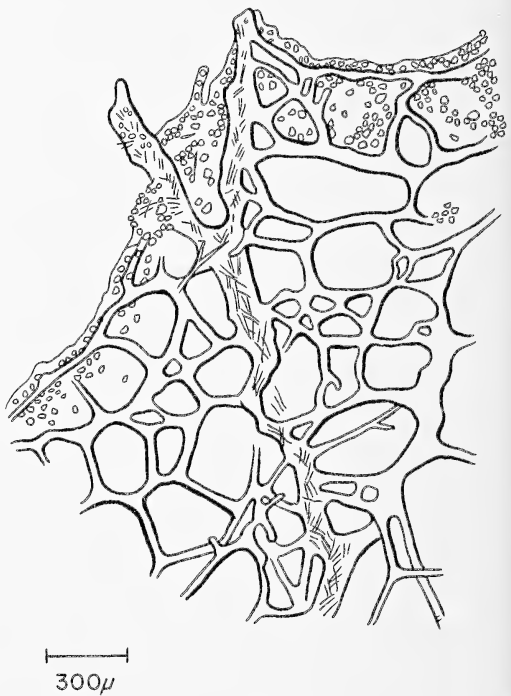


FIG. 11b. *Euryspongia lobata* n. sp. Portion of the fibre network.



possession of a eurypylous chamber system and a pronouncedly conulose surface this sponge could be referred to *Leiosella*.

There are no other species of *Euryspongia* known from this area. *Euryspongia phlogera* de Laubenfels (USNM 22952) is not a dysideid.

#### ORDER HAPLOSCLERIDA Topsent

#### FAMILY HALICLONIDAE de Laubenfels

#### GENUS HALICLONA Grant

#### *Haliclona velinea* (de Laubenfels)

Fig. 12

*Acervochalina velinea* de Laubenfels, 1954, p. 52, fig. 30.

? *Acervochalina finimita* Ridley, 1884, p. 399.

non *Chalina finimita* Schmidt, 1870, p. 33.

OCCURRENCE: Sta. 25.

DESCRIPTION: Only one small specimen of this sponge was collected; it was growing upon a branch of coral but became detached during collection. The habit is thickly encrusting; the sponge, which appears to be entire, is 1.7 cm long, 0.6–1.5 cm wide, 0.8 cm high.

COLOR: In alcohol, sandy except for a thin greyish-black surface layer.

TEXTURE: Relatively soft, easily compressible.

SURFACE: Irregular owing to incorporated calcareous debris. Where the darkly pigmented dermal membrane is entire, the macroscopic appearance is smooth, even slightly slimy. Under low magnification small surface conules are apparent. No pores or oscules are visible.

SKELETON: A reticulation of very fine spongin fibres which have no regular arrangement. Thicker ascending fibres are usually simple, but often two will unite and later diverge. Most connecting fibres arise at right angles to the ascending fibres but there are many exceptions, particularly in the deeper regions of the sponge where the fasciculation of primary fibres and branching of secondaries is common. Primary fibres are 16–24 $\mu$  in diameter and contain two, occasionally three, rows of oxeas; secondary fibres are 5.0–8.5 $\mu$  in diameter and never contain more than one spicule row. Spicules are also abundant interstitially.

SPICULES: Extremely fine, slightly curved

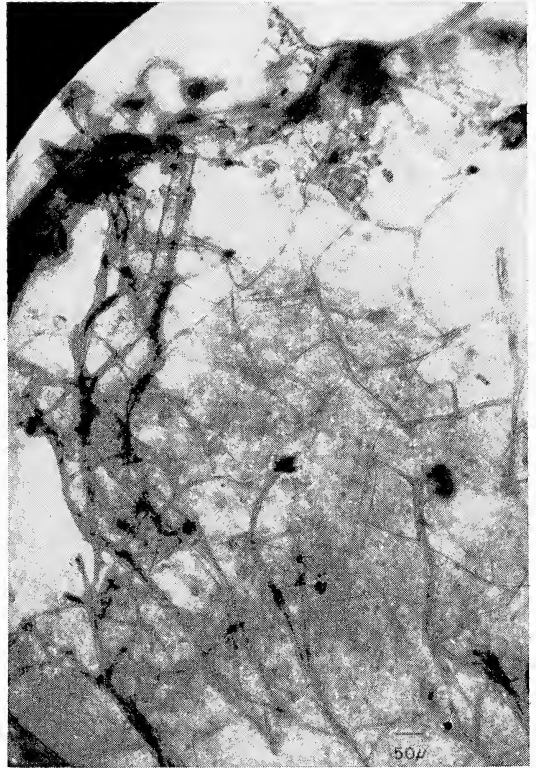


FIG. 12. *Haliclona velinea* (de Laubenfels). Photomicrograph showing the network of fine fibres, the conulose surface, and the darker dermal layer.

oxeas are the only spicules present.

DIMENSIONS: 88–102  $\times$  1.2–2.5 $\mu$ .

ECTOSOME: No ectosome is differentiated save the pigmented dermal membrane, 12–15 $\mu$  thick.

ENDOSOME: Fleshy and contains abundant spherical flagellate chambers 25–30 $\mu$  in diameter.

DISCUSSION: De Laubenfels (1954) states that spicules were sparse in this species; this is not the case in either the present specimen or the holotype (USNM 22854). Burton (1934: 529) puts forward a convincing argument for synonymizing *Acervochalina* Ridley with *Haliclona* Grant, and in doing so reverses his earlier (1927) decision to retain *Acervochalina* as a genus of the pachychalinid group lacking a dermal skeleton. When Ridley set up *Acervochalina* he named *Chalina limbata* Montagu (per Bowerbank) as the type. His generic diagnosis contains no reference to the presence of

a dermal skeleton, but Bowerbank (1865:373) distinctly mentions the dermal skeleton in this sponge. If Bowerbank's description is correct then *Acervochalina* cannot be synonymous with *Haliclona*; one can only assume that Burton, having access to Bowerbank's specimens, has checked this point.

Copious slime production is the character used by de Laubenfels (1954) to distinguish between *Acervochalina* and *Haliclona* but this, as Burton (1934) points out, is hardly ground for generic distinction.

It is probable that de Laubenfels' statement regarding Ridley's specimens of *Acervochalina finimita* (Schmidt) is correct, and that the North Australian specimens should be synonymized with *A. velinea* de Laubenfels. Only one statement in Ridley's description leaves this in doubt; he mentions stout primary fibres, but gives no measurements. Only reference to Ridley's specimens can decide this synonymy, but in terms of distribution, de Laubenfels' suggestion seems very likely to be correct.

DISTRIBUTION: Marshall Islands (de Laubenfels); Torres Strait, Queensland (Ridley).

*Haliclona koremella* de Laubenfels

*Haliclona koremella* de Laubenfels, 1954, p. 59, fig. 34.

OCCURRENCE: Sta. 10, 35.

REMARKS: The two specimens differ from the holotype in the dimensions of the fibres and in the number of spicule rows incorporated in primary and secondary fibres (Table 1).

DISTRIBUTION: Palau Islands (de Laubenfels).

GENUS *Cribrochalina* Schmidt

*Cribrochalina olemda* de Laubenfels

Fig. 13

*Cribrochalina olemda* de Laubenfels, 1954, p. 77, fig. 47, pl. IV, fig. a.

OCCURRENCE: Sta. 135.

REMARKS: De Laubenfels (1954) emphasized the difficulty of being certain that *Cribrochalina olemda* is not synonymous with some earlier described sponge since, in many early works, characters of the skeleton were described poorly, if at all, the tubular shape often being considered sufficient for identification. *C. olemda* appears, however, to be sufficiently distinct from such similar species as *Spinosella infundibuliformis* Lendenfeld to be considered a new species.

The single Palau specimen conforms closely to the type description. De Laubenfels was in some doubt as to the correct generic position of this sponge. Topsent (1920) has redescribed the type of *Cribrochalina*, *C. infundibula* Schmidt, and when his description is combined with Schmidt's type description, *Cribrochalina* emerges as a cup or funnel-shaped sponge, with concentric lines on the internal surface, having a complex multispicular network of vertical fibres, a well-defined system of subdermal cavities, and a protoplasmic dermal membrane containing no dermal skeleton.

*C. olemda* answers perfectly to this redefinition of *Cribrochalina*, having a faint pattern of concentric lines on the inner face of the tube, fasciculate fibres, protoplasmic dermis, and subdermal cavities. (This feature is not mentioned

TABLE 1

SPECIMEN	DIAMETER OF FIBRES		NO. SPICULE ROWS IN FIBRES	
	Primary	Connecting	Primary	Connecting
Sta. 10	32-87 $\mu$ (63 $\mu$ )	12-50 (29 $\mu$ )	10-20 rows	7-12 rows
Sta. 35	18-50 $\mu$ (25 $\mu$ )	10-32 (16 $\mu$ )	6-16 rows	3-12 rows
USNM 23129	100 $\mu$	15 $\mu$	4-7 rows	usually none

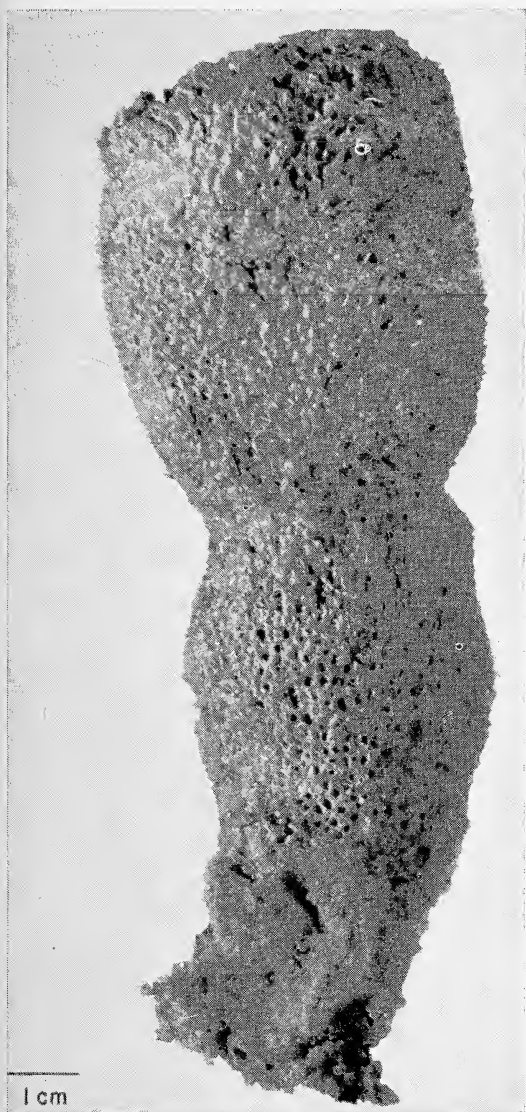


FIG. 13. *Cribrochalina olemda* de Laubenfels. Sta. 135.

by de Laubenfels and is visible only in specimens preserved in alcohol.)

DISTRIBUTION: Palau Islands (de Laubenfels).

GENUS *Xestospongia* de Laubenfels

*Xestospongia* de Laubenfels, 1932, p. 115.

*Neopetrosia* de Laubenfels, 1949, p. 10.

*Neopetrosia* de Laubenfels, 1954, p. 81 pars.

*Xestospongia exigua* (Kirkpatrick)

Fig. 14*i, ii, iii*

*Petrosia exigua* Kirkpatrick, 1900, p. 139, pl. XII, fig. 7; pl. XIII, fig. 4.

*Xestospongia exigua* de Laubenfels, 1949, p. 126.

non *Xestospongia sapra* de Laubenfels, 1954, p. 79, fig. 48.

*Neopetrosia pandora* (pars.) de Laubenfels, 1954, p. 81, fig. 49.

OCCURRENCE: Sta. 10, 47, 100.

DESCRIPTION: One specimen (Sta. 47) of this species is an erect sponge with numerous slender branches which sometimes anastomose; the other two are repent, with extremely irregular stout branches (Table 2).

SURFACE: Characterized by a reticulate pattern formed by the ascending endosomal columns which fan out distally and support the aspiculous dermal membrane. This pattern is uniformly evident in two specimens (Sta. 47 and 10) where the endosomal spicule tracts are narrower and the texture of the sponge is correspondingly softer; it is less pronounced but still visible in the third specimen. All of de Laubenfels' specimens of *Neopetrosia pandora* show this reticulation; it is also plain in his specimen of *Xestospongia exigua* from Yap, and was described by Kirkpatrick (1900) for the type specimen of *Xestospongia exigua*. The illustrations of *Petrosia similis* Ridley and Dendy (Pl. III, figs. 3, 4, 6), although lacking in detail, convey the impression of a reticulate surface as is described in the text.

SKELETON: In all three specimens the skeleton is basically an isodictyal reticulation with unispicular to multispicular ascending tracts developed to varying degrees. In the specimen from Sta. 100 these tracts are abundant and up to 300 $\mu$  wide. In other specimens tracts, 36–50 $\mu$ , six to eight spicules wide, are common; larger tracts up to 100 $\mu$  wide occur infrequently. In all cases numerous spicules occur usually aligned parallel to the ascending tracts.

Faint traces of spongin occur distributed sporadically along some of the ascending tracts. Immediately below the surface the ascending tracts fan out into brushes, 62–187 $\mu$  across, the outer spicules of which project slightly beyond the dermal membrane.

TABLE 2

CHARACTERISTIC	STA. 10	STA. 47	STA. 100
Color in life	blue		
Color in alcohol	greyish-brown externally (rY 4/2), reddish-brown internally (YR 4/6)	brown (γY-R 4/2)	pale brown (Y-R-Y 6/4)
Branch height	repent	mostly broken but greater than 20 cm	
Branch diameter	almost massive in form owing to frequent anastomoses 0.9–2.5 cm	0.4–1.2 cm always cylindrical or oval	extremely irregular often flattened 0.6–3.0 cm
Texture	firm, just compressible	firm, just compressible	cork-like, extremely brittle
Oscule diameter	1.2–2.5 mm	1.0–2.5 mm	0.8–4.0 mm
Spicule dimensions	105–132 × 3.0–5.5μ	99–126 × 1.5–5.0μ	105–130 × 3.5–5.5μ

DISCUSSION: The initial diagnosis of *Xestospongia* de Laubenfels (1932) reads, "characterized by having only oxeas as spicules and these so abundant that any reticulate arrangement is obscured; there is no special dermal skeleton." On the same page, in the description of the type species, *Xestospongia diprosopia*, an endosomal reticulation prominent enough to enable measurements of the meshes is described. A second species, *Xestospongia vanilla*, described in the same work conforms more closely to the generic diagnosis.

It is difficult to see the differences between *Xestospongia* de Laubenfels and *Neopetrosia* de Laubenfels if only the generic diagnoses are considered. *Neopetrosia*, with type species *Haliclona longleyi*, is defined as "differing from *Haliclona* by having a smoother surface, more brittle consistency and other important differences which we are not yet ready to discuss."<sup>5</sup> The erection of *Neopetrosia* was premature and it remains an incompletely defined genus.

It is unquestionably correct that there are at least two separate groups of sponges in *Petrosia*, some with the spiculation of the type species (*Petrosia dura* (Schmidt)) possessing a der-

mal skeleton and having a rock-like texture, others with oxeas, no dermal skeleton, retaining the stony texture and having little or no trace of a reticulate skeleton. The erection of *Xestospongia* for the latter group was thus justified, but the genus requires redefinition in terms of western Pacific material which has been subsequently assigned to it.

The specimen from Yap (USNM 22733), described as *Xestospongia exigua* (Kirkpatrick) by de Laubenfels (1949), is identical except in form with the holotype of *Neopetrosia pandora* de Laubenfels 1954 (USNM 23046) and is distinctively different in spiculation from *Xestospongia sapra* de Laubenfels. *Xestospongia sapra* has oxeas, strongyles, and styles of irregular, curved, even wavy form and has a microconulose surface. De Laubenfels (1954) stated that his specimens of *X. exigua* and *X. sapra* both belonged to *sapra*; this is not the case.

In describing *Neopetrosia pandora*, de Laubenfels mentioned the great variability of his specimens in details of spiculation and in habit. This can be endorsed from a study of the type series and the Palau collections. In view of this variability it is difficult to see why de Laubenfels did not relate his Yap specimen of *X. exigua* to this complex. It is possible that de Laubenfels described more than one species under *N. pandora*; specimen 403 (USNM 23024)

<sup>5</sup> This refers to Bergmann's work on the sterols of sponges. Those of *H. longleyi* were distinctive; unfortunately no further data have been produced which pertain to this species or to the genus *Neopetrosia*.

is quite removed from all others by its spiculation. Apart from this all specimens can be regarded as belonging to one variable species. The question is, should this be a species of *Xestospongia* or of *Neopetrosia*? Either would require expanding the generic diagnosis. In addition to the basic reticulate structure, the Palau specimen from Sta. 100 has large tracts of vertically aligned spicules up to  $275\mu$  wide and is thus approaching the type of structure which *Xestospongia* should possess and which is exemplified in *X. vanilla* and *X. (Petrosia) coraloides*. This particular specimen is almost stony and brittle. However, the differences which separate these sponges are only differences of degree. Spicule tracts are present, but are much narrower in the specimens from Sta. 10 and

Sta. 47, and these specimens although firm and brittle, could not be described as stony.

It is suggested that the definition of *Xestospongia* should be rephrased to include sponges like the type species, where a distinct reticulate skeleton is present but where accumulation of spicules may be so great as to obscure this in parts or in all of the sponge except the subdermal region. Many sponges assigned to this genus have a reticulate surface pattern.

*Neopetrosia* does not differ in any way from *Xestospongia* as defined above and as understood by de Laubenfels (1950:49). The only species assigned to *Neopetrosia* to date are *Haliclona longleyi* de Laubenfels, the type species, *Neopetrosia pandora* from the Palau Islands, and *Petrosia similis* Ridley and Dendy; all three

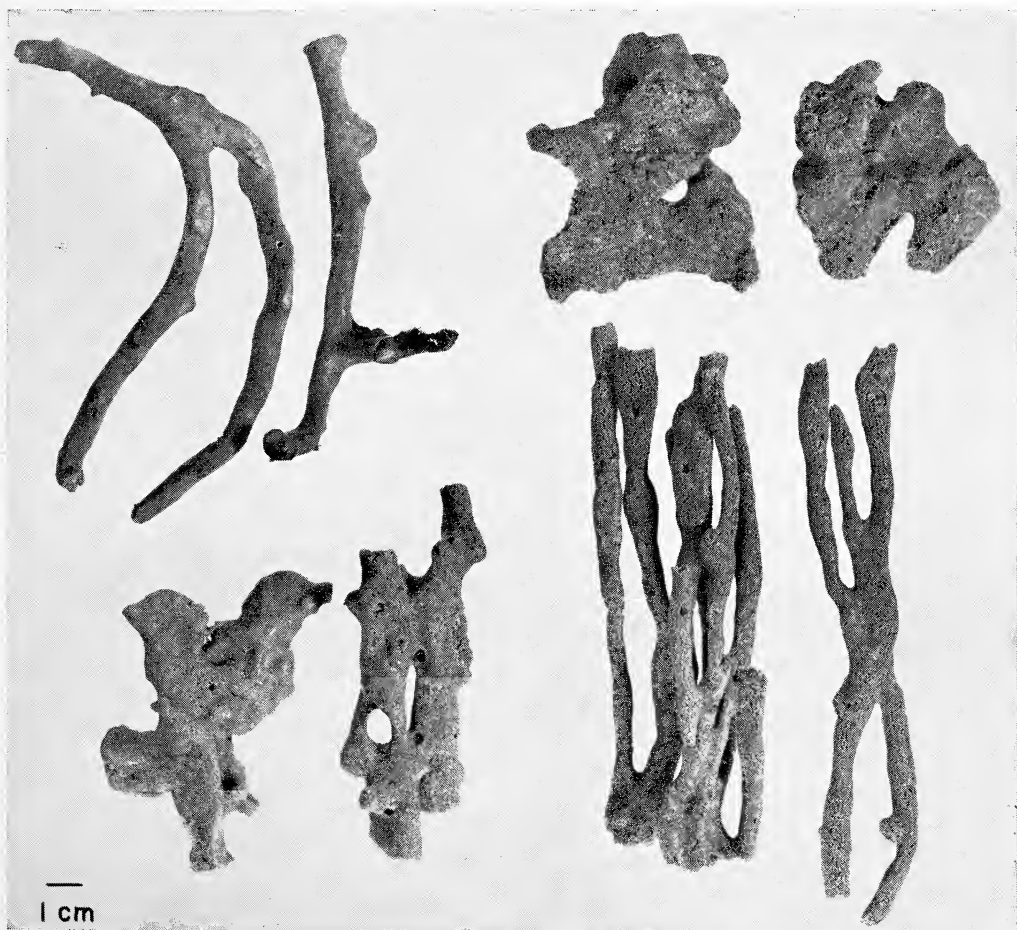


FIG. 14. *Xestospongia exigua* (Kirkpatrick). (i) Upper right, Sta. 100. (ii) Lower left, Sta. 10. (iii) Lower right, Sta. 47. *Clatbria cervicornis* (Thiele). (iv) Upper left, Sta. 220B.



FIG. 15a. *Callyspongia subarmigera* (Ridley). Sta. 125.

species can be transferred to *Xestospongia*, with *N. pandora* falling to *X. exigua* (Kirkpatrick).

**DISTRIBUTION:** Christmas Island (Kirkpatrick); Yap Archipelago, Palau, Marshall Islands (de Laubenfels).

#### FAMILY CALLYSPONGIIDAE de Laubenfels

GENUS *Callyspongia* Duchassaing and Michelotti

*Callyspongia subarmigera* (Ridley)

Fig. 15a, b, c

*Cladochalina subarmigera* Ridley, 1884, p. 397, pl. XXXIX, fig. H, pl. XLI, fig. L.

*Pachychalina fibrosa* var. *gracilis* Wilson, 1925, p. 412.

*Callyspongia subarmigera* Burton, 1934, p. 540.

**OCCURRENCE:** Sta. 125.

**DESCRIPTION:** A repent sponge composed of unbranched cylindrical stems 4.0–9.0 mm in diameter, bearing prominent spinous processes and having oscules, 2.5–3.5 mm, arranged along the upper surface.

**SURFACE:** Smooth, the pattern of the dermal skeleton somewhat obscured by fine coral sand.

**SKELETON:** In all essential features the skeleton conforms with the type description of this species (Ridley, 1884:397). The construction of the endosomal skeleton is essentially radial with polyspicular primary fibres diverging from an excentric hub. Secondary fibres arise at right angles to these. Between the rectangular meshes of the secondary fibres a fine system of tertiary, mono- or bi-spicular fibres ramifies in irregular

fashion. The stout endosomal fibre system terminates abruptly immediately below the surface. Both primary and secondary fibres give rise to a system of fine vertical fibres which support the primary and secondary meshes of the dermal skeleton. These supporting fibres are of equivalent diameter to the primary meshes of the dermal skeleton.

*Fibre dimensions* (in  $\mu$ ).

Skeleton	Primary	Secondary	Tertiary
Dermal	12–28 meshes 300–375	4–12 meshes 55–78	none
Endosomal	37–60	12.5–50	2–15

The endosome incorporates much debris and a few interstitial spicules.

**SPICULES:** Extremely fine strongyles, 72–90  $\times$  0.8–1.5  $\mu$ . In a few cases slightly stouter tornote oxeas occur.

**DISCUSSION:** *Callyspongia subarmigera* Ridley is a well-characterized species; the type description differs from the Palau specimen only in possessing tornote oxeas exclusively, where the Palau sponge has strongyles predominantly and just occasional oxeas. In this respect the



FIG. 15b. *Callyspongia subarmigera* (Ridley). Section of the skeleton showing the radial primary fibres and complex network of connecting fibres. The dermal network shows at the upper right.



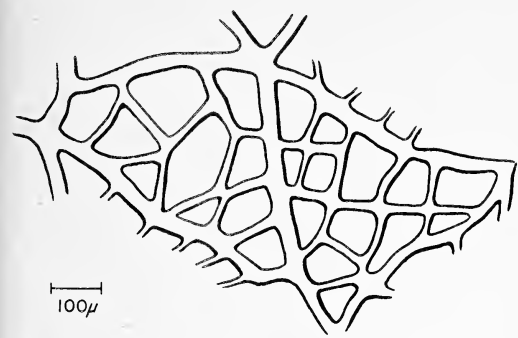


FIG. 15c. *Callyspongia subarmigera* (Ridley). Detail of the dermal skeleton.

latter is reminiscent of *Callyspongia armigera* from the West Indies.

*Pachychalina fibrosa* var. *gracilis* Wilson has stouter fibres and wider meshes throughout than does the Palau specimen. In construction and habit the two compare closely, and both have strongyles, those in Wilson's specimen being slightly stouter than those of the Palau specimen and nearer in this respect to the type. In all features except the possession of strongyles *Pachychalina diffusa* var. *affinis* Hentschel is close to *C. subarmigera* (Ridley).

DISTRIBUTION: Northern Australia (Ridley, Burton); Philippines (Wilson).

*Callyspongia ridleyi* Burton

Fig. 16a, b

*Callyspongia ridleyi* Burton, 1934, p. 543, fig. 7, a, b.

OCCURRENCE: Sta. 220A (six specimens).

DESCRIPTION: The specimens are probably all part of one large colony which is similar to that described as *Callyspongia ridleyi* by Burton. Both species of *Callyspongia* described here exhibit a marked tendency toward the formation of strongylote spicules. In the specimens of *C. ridleyi* strongyles are approximately 5% of the spicule total; their dimensions are equivalent with those of the tornote oxeas,  $78-89\mu \times 2.0-3.5\mu$ .

Fibre dimensions (in  $\mu$ ).

Skeleton	Primary	Secondary
Dermal	15-37 (26)	4.5-16 (11.5)
Endosomal	20-28 (25)	5-16.5 (12)

Australian specimens of *Callyspongia ridleyi* have substantially larger spicules ( $200 \times 8\mu$ ) than the Palau specimens but compare very closely in all other respects. In the absence of specimens from intervening localities it is not possible to evaluate the significance of these spicule differences.

DISTRIBUTION: Northeastern Australia (Ridley, Burton).

FAMILY DESMACIDONIDAE Gray

GENUS *Gelliodes* Ridley

*Gelliodes gracilis* Hentschel

*Gelliodes gracilis* Hentschel, 1912, p. 395, pl. XXI, fig. 49.

*Gelliodes gracilis* de Laubenfels, 1954, p. 89, fig. 53, pl. V, fig. b.

OCCURRENCE: Sta. 125.

REMARKS: This specimen is identical with the Palau sponge described by de Laubenfels and assigned to this species (Bishop Museum 125). De Laubenfels expressed doubts as to whether *G. gracilis* should remain in *Gelliodes*, but gave no reasons for this. The Palau specimens have the fleshy conulose surface, fibrous structure, and spiculation of the type species of *Gelliodes* and appear to be correctly placed in this genus. The correspondence between the Palau specimens and *G. gracilis* Hentschel is close; the two possibly differ in surface features



FIG. 16a. *Callyspongia ridleyi* Burton. Sta. 220A.

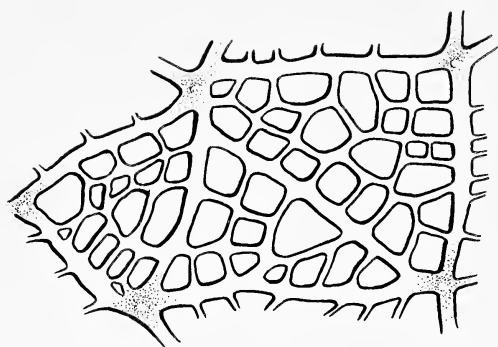


FIG. 16b. *Callyspongia ridleyi* Burton. Detail of the dermal skeleton.

but these are neither discussed in detail nor figured by Hentschel.

DISTRIBUTION: Malay Area (Hentschel); Palau Islands (de Laubenfels).

ORDER POECILOSCLERIDA Topsent

SUBORDER PHORBASIFORMES de Laubenfels

FAMILY ADOCIIDAE de Laubenfels

GENUS *Adocia* Gray

*Adocia turquoisia* de Laubenfels

*Adocia turquoisia* de Laubenfels, 1954, p. 106, fig. 67.

OCCURRENCE: Sta. 92.

DESCRIPTION: The specimen is damaged. It grows as a system of irregular tubes, each with a terminal oscule; some tubes are laterally placed.

COLOR: In alcohol, pale creamy yellow (yY-R 6/4).

TEXTURE: Soft, the sponge easily compressible.

SURFACE: Smooth, and has a plain, but irregular, reticulate pattern outlined by stout tangential fibres in a subdermal position. Oscules are large, 4.0–5.0 mm in diameter, and are terminal on all branches.

SKELETON: The dermal skeleton is a unispicular isodictyal reticulation of oxeas with regular triangular meshes,  $75\text{--}87\mu$  from apex to base. The unispicular isodictyal pattern is repeated in the endosomal skeleton, where small patches of spongin cement the spicule points. Running vertically through the endosome are occasional multispicular tracts,  $12.5\text{--}62\mu$  in diameter. These only rarely branch in the body of the sponge.

Immediately below the dermal membrane they branch repeatedly in a tangential plane and form a conspicuous and irregular mesh in which the large tracts are up to  $100\mu$  in diameter. The finer branches of this subdermal network delimit the pore areas which are overlain by the dermal skeleton.

SPICULES: Slightly curved or straight, evenly pointed oxeas  $70\text{--}100 \times 1.8\text{--}4.5\mu$ .

ENDOSOME: Contains abundant, spherical, flagellate chambers,  $30\text{--}36\mu$  in diameter. Abundant developing egg cells are present; these are oval, up to  $350 \times 250\mu$ , with extremely prominent nuclei and granular cytoplasm.

DISCUSSION: The type description of *Adocia turquoisia* de Laubenfels makes no reference to the multispicular tracts below the dermal membrane. These are present, however, in the paratype (Bishop Museum 149), and the form of the latter is not incompatible with that of the fragments from the Palau Is. The oscules are similar, terminal on poorly developed lobes in one case, aligned along the upper surface of a branch in the other.

DISTRIBUTION: Palau Islands; Marshall Islands (de Laubenfels).

GENUS *Toxadocia* de Laubenfels

*Toxadocia violacea* de Laubenfels

Fig. 17

*Toxadocia violacea* de Laubenfels, 1950, p. 16, fig. 9.

OCCURRENCE: Sta. 10.

DESCRIPTION: The sponge is loosely encrusting (0.8 cm thick) upon specimens of *Coelocarteria singaporense* and is badly damaged; only one or two fragments of the dermal membrane remain. No oscules are visible.

COLOR: In alcohol, grayish.

TEXTURE: Extremely soft, and tends to fall apart at the touch.

SURFACE: Smooth; the dermal membrane supports a tangential dermal skeleton arranged as a unispicular isodictyal reticulum.

SKELETON: Basically a unispicular isodictyal reticulation the regularity of which is broken in places by alignment of spicules at right angles to the surface. Where this aggregation of spicules occurs the matrix is always more darkly



staining than usual and elongate fibrous cells are concentrated with their long axes parallel to the spicules. These columns usually traverse approximately one third of the thickness of the sponge.

The mesh of the endosomal reticulum is 100–125 $\mu$ ; three to six spicules join at the corners of the mesh and conspicuous patches of spongin occur at all intersections. In the deeper parts of the sponge the reticulum is less regular, and

occasionally three to four spicule lengths will be encased in spongin, simulating a fibrous structure.

**SPICULES:** *Megascleres*. Oxeas, straight or slightly curved, evenly tapered, 132–158  $\times$  1.8–6.0 $\mu$ .

*Microscleres*. Toxas, of relatively open form with little or no reflexure of the tips, 25–96 $\mu$  (60 $\mu$ ).

**DISCUSSION:** This rather fragmentary specimen is identified with *Toxadocia violacea* from Hawaii chiefly upon spicule characters. Spiculation and violet color are the distinguishing features of *T. violacea*. The toxas of the type (USNM 22752) and the Palau specimen are closely comparable in shape, and the size range of the oxeas is close.

**DISTRIBUTION:** Hawaii (de Laubenfels).

#### GENUS *Orina* Gray

*Orina sagittaria* (Sollas)

Fig. 18a, b, c

*Gellius sagittarius* Sollas, 1902, p. 212, pl. XV, fig. 7.

*Adocia sagittaria* Burton, 1934, p. 538.

**OCCURRENCE:** Sta. 12, 60.

**DESCRIPTION:** The habit of this sponge is most distinctive, with a massive base producing one to three stout fistules from the upper surface. These anastomose and then subdivide terminally into a number of finer tubes which expand into an oval structure on which pores are located. The walls of the tubes contain vertical spicule tracts, and the terminal expansion is merely an open network of irregular tracts with little or no reticulate structure and a minimum of soft tissues. Lateral branches may arise from the upright fistules. One such branch shows a terminal expansion which is not plainly set off from the tube: the walls merely become transparent, the fibres are prominent, the surface hispid, and the lumen a little wider. This is interpreted as a developmental stage of the typical structure described above. The function of these terminal caps is unknown; they were often observed free floating in the field and may possibly be an asexual dispersal structure. There is noth-

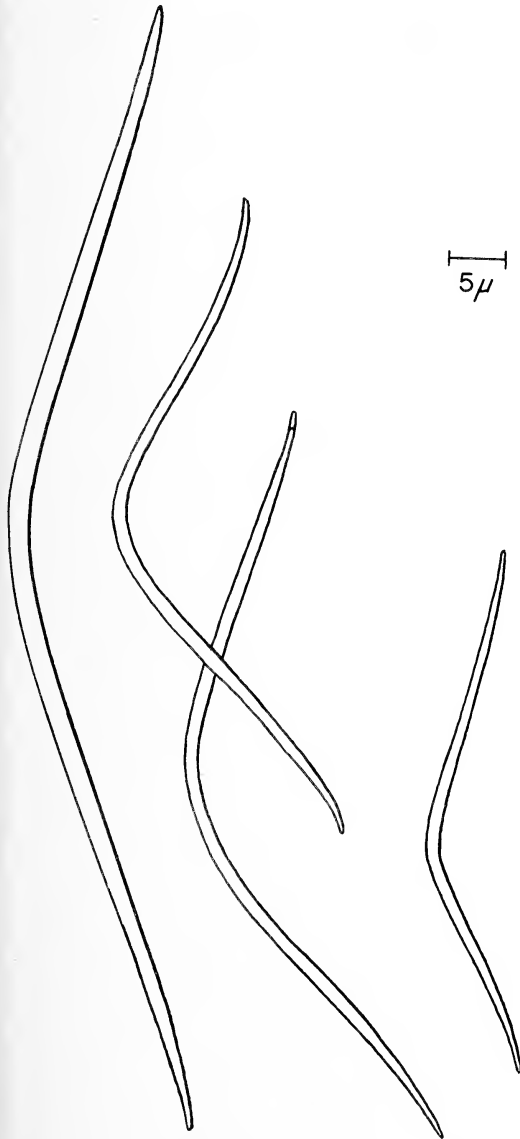


FIG. 17. *Toxadocia violacea* de Laubenfels. Toxa.

ing in their morphology to suggest this, however, and the very restricted occurrence of the sponge does not suggest the presence of an elaborate dispersal mechanism.

**DIMENSIONS:** *Basal mass*, 4.5 cm long; 4.0 cm high; 3.0 cm thick. *Fistules*, 8.5 cm high; 0.65–0.75 cm in diameter, 1.1 cm after anastomosis, walls 1.2 mm thick; lateral branch, 2.2 cm high; 0.5 mm in diameter, walls, 0.3 mm thick. *Terminal expansion*,  $1.5 \times 1.0$  cm, 0.8 cm high.

**COLOR:** In life, bright red; in alcohol, brown (Sta. 12) (yY-R 4/2) or dull reddish-brown externally, between (RY-R 4/4) and (RY-R 3/4), to pale brown internally (rY-R 5/4).

**TEXTURE:** Firm and brittle with respect to the fistules and the dermis of the base; the endosome of the latter is soft and easily crumbled.

**SURFACE:** Smooth, except at the tips of branches or on the pore areas where fibres

project and render the surface conulose and slightly hispid. No oscules are visible, but numerous skeletal pores are discernible on the terminal expansions of the fistules.

**SKELETON:** The skeletal pattern of this sponge is a curious composite of an irregularly isodictyal network with spicule tracts produced in the fistules and the terminal caps and of a more or less halichondroid skeleton, with spicules in confusion, lining all large canals in the endosome. The dermal skeleton is made up of tangentially placed oxeas with no regular arrangement and of abundant sigmas. Below the dermis is an extensive subdermal space system, 700–800 $\mu$  deep, across which only isolated oxeas extend to support the dermal skeleton. These oxeas are part of the irregular reticulation which extends throughout the sponge and which is the basic endosomal skeleton. Most of the component spicules of the endosomal reticulum, except in the subdermal region, are coated with a coarsely granular dark brown material.<sup>6</sup> In addition to this skeletal framework, dense aggregations of oxeas line all major canals. These spicules are chiefly disposed at right angles to the edges of the canals and give the sponge tissue an irregularly lobulate appearance in section.

In the fistules the skeleton shows little organization except toward the production of longitudinal tracts. These become extremely pronounced in the expanded tips of the fistules where few extraneous spicules occur.

**SPICULES:** *Megascleres*. Oxeas, slightly curved often a little wavy, evenly tapered,  $325\text{--}375 \times 5.5\text{--}10\mu$ .

*Microscleres*. Sigmas, with abruptly recurved tips and often centrally angulate,  $10.5\text{--}20.5\mu$ . Toxa, of open form, either straight-sided or with slightly reflexed tips,  $36\text{--}50\mu$ .

**DISCUSSION:** This specimen is the most complete so far recovered of this species; however, the more that is known of its morphology the more difficult it becomes to assign conclusively to a genus. The form of the sponge is peculiar, particularly in the production of fibrous terminal expansions to many of the fistules. Most likely these are pore sieves, and some tubes may termi-



FIG. 18a. *Orina sagittaria* (Sollas). Sta. 60.

<sup>6</sup> This appears to be similar to the structure described for *Gellius luridus* by Lundbeck (1902:64).

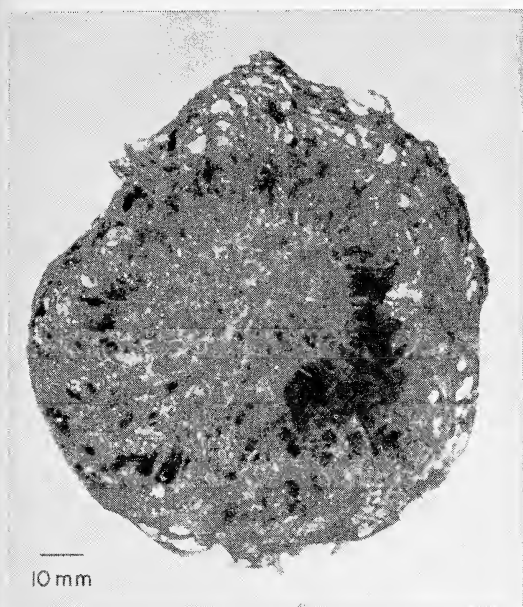


FIG. 18b. *Orina sagittaria* (Sollas). Apical view of one of the detachable caps from the oscular tubes.

nate in oscules. None of the latter have been observed. Careful study of the pore sieves must be done on fresh material since almost all soft tissues have fallen away from the fibres in alcohol-preserved material. The combination in this sponge of reticulate, fibrous, and confused skeleton underlines the difficulty of defining genera on skeletal pattern.

Burton (1934) has assigned *Gellius angulatus* var. *canaliculata* Dendy to this species but, in details of the skeleton and the size of the sigmas, the description of this sponge does not coincide with Sollas' description or the Palau specimens.

DISTRIBUTION: Malay area (Sollas); Great Barrier Reef (Burton).

#### GENUS *Kallypilidion* de Laubenfels

##### *Kallypilidion poseidon* de Laubenfels

*Kallypilidion poseidon* de Laubenfels, 1954, p. 110, fig. 70, pl. IX, fig. a.

OCCURRENCE: Sta. 67.

DISCUSSION: This species is well described by de Laubenfels (1954) and the single specimen from the Palau conforms in detail with the description and with the paratype (Bishop Museum 169). De Laubenfels (1950) erected the

genus *Neoadocia* for *N. mokuoloea* from Hawaii, a sponge which has adociid construction and spiculation, except for the addition of rapheids; the surface of this sponge is markedly punctate. *Neoadocia* and *Kallypilidion* are closely comparable; only color and shape separate the two genera.

DISTRIBUTION: Palau Islands, Marshall Islands (de Laubenfels).

#### GENUS *Pellina* Schmidt

##### *Pellina carbonaria* (Lamarck)

Fig. 19

*Spongia carbonaria* Lamarck, 1814, p. 375.

? *Thalasyias carbonaria* Duchassaing and Michellotti, 1864, p. 83, pl. XVII, fig. 4, pl. XIX, fig. 2.

*Pachychalina carbonaria* Arndt, 1927, p. 152, pl. 1, fig. 1, text fig. 13.

*Phloeodictyon carbonarium* Topsent, 1930, p. 26.

*Pellina carbonaria* de Laubenfels, 1936, p. 68, pl. 18, fig. 5.

*Pellina carbonaria* de Laubenfels, 1954, p. 101, fig. 63.

OCCURRENCE: Sta. 92, 133.

DISCUSSION: The two specimens have been compared closely with de Laubenfels' material from the same area (USNM 23113 and Bishop Museum M. 495) and with material from Ja-

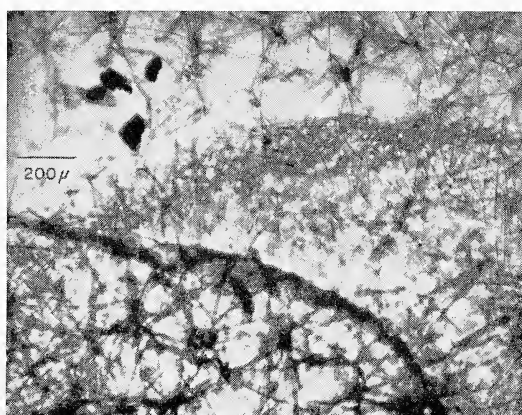


FIG. 18c. *Orina sagittaria* (Sollas). Section of the sponge showing the spongin coated spicule reticulum (lower left), the halichondroid skeleton (center right), and the open spicule reticulum in the subdermal position (upper).

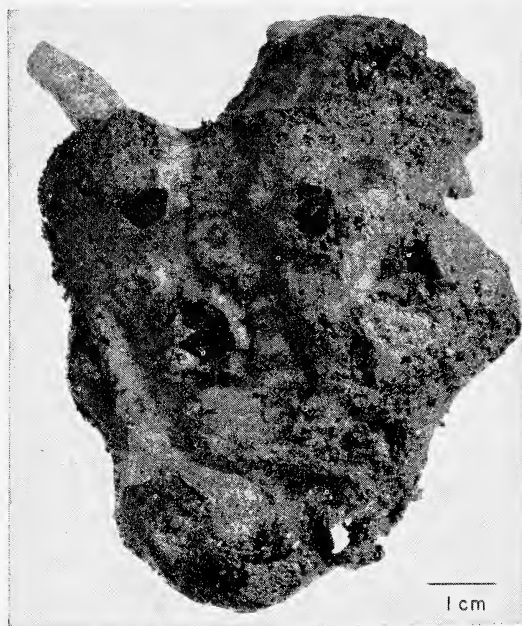


FIG. 19. *Pellina carbonaria* (Lamarck). Sta. 133.

maica in an attempt to find characters which will serve to differentiate between the West Indian and the Pacific populations assigned to *P. carbonaria*.

Only minor differences can be found. The spicules are consistently larger in the Pacific specimens and, as far as is known, these specimens do not produce the blue-black exudate in alcohol that characterises *Pellina carbonaria* from Jamaica. The dermis is more easily detachable in the Pacific specimens than in the Jamaican specimens, but this feature also characterises Lamarck's type from the West Indies (Topsent, 1930).

De Laubenfels considered that the Pacific specimens which he assigned to *P. carbonaria* were closer to the type description than were his specimens from the Tortugas. His suggestion was that Lamarck may have made an error in the locality of his specimen and that in fact *Pellina carbonaria* (Lamarck) may have been from the Pacific. There is, however, no evidence to support this contention. A comparison of the spicule size and shape characteristics in this species from the two areas (Table 3), reveals that the Jamaican specimen and the type are closely comparable, as are the three Palau speci-

mens. The differences between the two groups are, however, slight. De Laubenfels' specimens from the Tortugas have substantially smaller spicules but show the strongylote and stepped condition so common in specimens from other localities.

It is difficult to argue on morphological grounds that there are two species involved here. There are indications that studies of pigments could reveal differences which, in conjunction with the slight morphological discrepancies, would justify the use of a new name for the Pacific specimens. Ecological data on this species would be a valuable adjunct to morphological studies. *P. carbonaria* in Jamaica inhabits *Zostera* flats and rarely produces fistules; nothing is known of the habitat and range of growth forms of this sponge from the Pacific.

DISTRIBUTION: West Indies (Lamarck); Curaçao (Arndt); Jamaica (Hechtel); Palau Islands (de Laubenfels); Freemantle (W.A.?) (Carter 1882).

#### GENUS *Siphonodictyon* n. gen.

This genus is established for *Siphonodictyon mucosa*, the type species, and is closely related to *Phloeodictyon* Carter. It differs notably in lacking a bark-like dermal region, in the production of great quantities of mucus, in the complete lack of spongin, in the cryptic habit and in the possession of a dermal skeleton represented by brushes of oxeas. *Phloeodictyon aberrans* Dendy from New Zealand should also be included in this genus.

#### *Siphonodictyon mucosa* n. sp.

Fig. 20a, b

OCCURRENCE: Sta. 92 (Holotype, USNM 23697), 92A (three specimens).

DESCRIPTION: The basal portion of the sponge fills large cavities in coral and sends up several brittle cylindrical tubes which terminate in either sieve areas or oscules. Excessive quantities of mucus are secreted from the basal mass and apparently are exuded over the external surface of the oscular tubes during life. A thick layer of jelly-like mucus invests the sponge inside the cavity. It is difficult to be sure that this layer is external to the sponge since, in places, a crisp layer of tangential oxeas overlies the

TABLE 3

SPECIMENS	LARGER OXEAS ( <i>u</i> )	SMALLER OXEAS ( <i>u</i> )	DETAILS OF SHAPE
<i>Pellina carbonaria</i> Palau (de L., 1954) USNM 23113	254–287 × 11.6–14.6	212–237 × 3.3–5.0	strongyles, styles, and oxeas often stair-stepped, some mucronate. Usually curved, rarely straight.
Sta. 92. Palau	237–290 × 7.0–14.8	207–246 × 3.0–6.0	oxeas, styles, strongyles, stepped or mucronate, curved or rarely straight; fine spicules always oxeote.
Sta. 133. Palau	225–260 × 9.0–10.5	207–225 × 3.5–6.6	oxeas which can be almost mucronate; stepped or strongylote, always curved, can be centrally angulate.
Jamaica	220–237 × 8.0–10	212–220 × 2.5–4.5	oxeas stair-stepped, mucronate often strongylote, smaller spicules often typical oxeas, always curved.
Topsent, 1930 (redescription of Lamarck's type)	220–215 × 8.0–14		oxeas, curved, only very slightly fusiform.
De Laubenfels, 1936 Tortugas	164 × 4.5 (rarely 172 × 5)		strongyles, stair-stepped.
Arndt, 1927 Curaçao	190–242 × 7–10	190–242 × 7–10	oxeas.

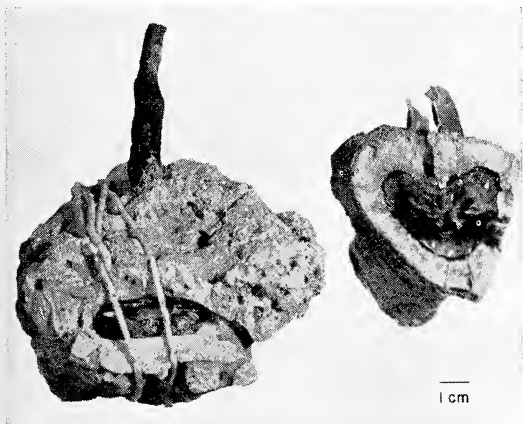


FIG. 20a. *Siphonodictyon mucosa* n. sp. Left, Sta. 92A; right, Sta. 92. Holotype. USNM 23697.

mucus and no dermal skeleton can be located at the inner boundary of the gel layer.

DIMENSIONS (Table 4).

COLOR: In life, black; in alcohol, dark brown (Y-R-Y 3/2) to pale brown (Y-R-Y 7/4) on the oscular tubes; the basal mass is pale brown (rY-R 5/4).

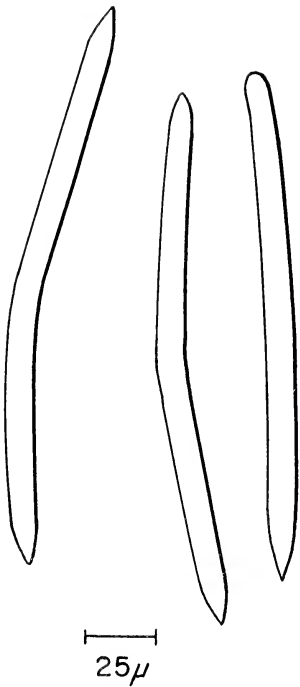


FIG. 20b. *Siphonodictyon mucosa* n. sp. Oxeas.

TEXTURE: The oscular tubes are brittle and incompressible; the body of the sponge is soft and gelatinous, easily torn.

SURFACE: All surfaces are smooth. Oscules are large and terminal on some of the erect tubes; pores are presumably restricted to the sieve ends of the remaining tubes.

SKELETON: A dermal skeleton is present in some areas of the oscular tubes in the form of an irregular reticulation overlying the fibres of the endosome. The meshes of this dermal reticulation are 275–500 $\mu$  from base to apex. On the basal portion of the sponge the dermal skeleton is developed as a tangential multispicular reticulum, present only in isolated places, external to the mucous layer.

The endosomal skeleton makes up almost the entire wall of the oscular tubes (900–1500 $\mu$  thick). The inner half of the endosome is occupied by stout fibres running longitudinally; these are 250–375 $\mu$  across and are connected at frequent intervals by stout transverse fibres, 62–125 $\mu$  in diameter.

The spicules are dense enough in some places to obscure the fundamental reticular pattern of the skeleton. Arising from this inner belt of fibres are numerous stout spicule brushes aligned at right angles to the long axis of the cylinder and running to the surface where they fan out and support the delicate dermal structures. These brushes are 300–750 $\mu$  long.

In the basal portion of the sponge the skeleton is somewhat confused and the details of structure are obscured by the abundance of darkly staining mucus. No spongin is associated with the skeleton and spongin A fibres appear to be absent from the ground substance of the endosome.

SPICULES: The spicules are stout, abruptly pointed oxeas, 194–212  $\times$  8.5–11.5 $\mu$ . There is considerable variation in shape: some are straight, some doubly curved or angulate, the majority are evenly curved. Styles are occasional.

FLAGELLATE CHAMBERS: These are abundant in the endosome, spherical, 18–20 $\mu$  in diameter.

MUCUS PRODUCTION: There is little development of soft tissue in the fistules and it appears that the production of mucus is entirely restricted to the base of the sponge. Mallory-stained sections of this region reveal numerous large oval darkly staining cells, 6.0–10 $\mu$  long, aggregated in groups of 10–20. These are probably secretory cells, but the preservation of the specimens did not permit use of any specific mucus stain.

DISCUSSION: There has been considerable confusion in the literature concerning the synonymy of *Oceanapia* Norman, *Rhizochalina* Schmidt, and *Phloeodictyon* Carter and the relationship of these sponges to the Coelosphaeriidae on the one hand and the Haplosclerida and Adociidae on the other. Since the genus *Siphonodictyon* is related to this group of sponges it is necessary to attempt to clarify the position.

Lundbeck (1902), after studying the holotypes of *Rhizochalina oleracea* and *R. carrotta*, was convinced that *Rhizochalina* should be reserved for Schmidt's original two species and that *Phloeodichyon* Carter should be used to accommodate all species referred to *Rhizochalina* by later authors. *Rhizochalina* possesses well developed spongin fibres containing short oxeas; in *Phloeodictyon* relatively little spongin is associated with spicule tracts and the oxeas are larger. Lundbeck separates *Oceanapia* (type species, *Desmacidon jeffreysi* Bowerbank) from

TABLE 4

SPECIMEN		LENGTH OF TUBES FROM BASE TO TIP	DIAMETER OF TUBES	OVER-ALL LENGTH, BREADTH, AND THICKNESS OF SPONGE	THICKNESS OF MUCOUS LAYER
Sta. 92 <sup>7</sup>		Broken	0.8 cm	4.0 $\times$ 3.5 $\times$ 2.9 cm	1.0–1.8 mm
Sta. 92A	1.	3.5 (2.1) cm 3.2 cm	0.8 cm	4.5 $\times$ 1.5 $\times$ 2.8 cm	1.5–3.0 mm
	2.	2.0 cm 7.4 (5.2) cm	1.1 cm base 0.6 cm tip	—	—

<sup>7</sup> This specimen is designated as holotype.

*Phloeodictyon* on the basis of the presence of sigmas in the former. The effect of Lundbeck's revision was to disperse the genera of Carter's *Phloeodictyina* through three separate divisions of the Haplosclerida by placing great emphasis on spiculation and amount of spongin present.

Spiculation is obviously not an adequate criterion for the wide separation of these genera. Topsent (1920), in his redescription of Schmidt's specimens of *Rhizochalina oleracea* and *R. carotta*, emphasizes the presence of sigmas in *R. carotta* and their absence from *R. oleracea*. These sponges are from the same locality, they are similar in form and construction and differ only in the presence or absence of sigmas. Lundbeck was prepared to leave these two species in *Rhizochalina* and at the same time to refer *Oceanapia* to the Gelliinae because it possessed sigmas.

Dendy (1921) recognizes all three genera and retains the group *Phloeodictyinae* as a subfamily, widely separate from the more typical Coelosphaerid genera (e.g., *Amphiastrella*, *Coelosphaera*) which he previously (1905) included with the *Phloeodictyinae*.

Burton (1934) considers *Rhizochalina* and *Phloeodictyon* to be synonyms of *Oceanapia*. He does not consider differences in microscle content, amount of spongin and anatomy of fistules to be sufficiently significant to warrant maintaining the three genera. Burton concurs with Dendy in placing *Oceanapia* in the family Haploscleridae but does not recognize the Coelosphaerae as a separate section of the Ectyoninae. For example, he treats *Coelosphaera* as a myxiliid and *Coelocarteria* as a clathriid.

De Laubenfels (1936) has confused the Coelosphaerae and the *Phloeodictyinae*. He grouped them in one family, Coelosphaeridae, which he placed close to the Adociidae. The only possible justification for this view is that the spherical form and production of fistules is common to all genera involved. *Phloeodictyon* was considered by de Laubenfels to be a synonym of *Rhizochalina*, but *Oceanapia* was maintained because it possessed sigmas.

Of the four different treatments of these sponges outlined above, that proposed by Dendy is clearly the most logical and takes greatest note of the details of morphology of the speci-

mens concerned. In keeping with this view *Siphonodictyon* is placed in the Adociidae.

Burton (1934) has queried the value of the section Coelosphaerae as used by Dendy. It is probable that Burton is correct and that the genera of this group should be widely dispersed throughout the Poecilosclerida. This step is not taken here since many genera in no way connected with the region under consideration are involved.

#### FAMILY COELOSPHAERIDAE Hentschel

##### GENUS *Coelocarteria* Burton

*Coelocarteria* Burton, 1934, p. 563.

*Ichnodonax* de Laubenfels, 1954, p. 111.

##### *Coelocarteria singaporense* (Carter)

*Phloeodictyon singaporense* Carter, 1883, p. 326, pl. XIII, fig. 7.

*Rhizochalina singaporensis* var. Ridley, 1884, p. 421, pl. XII, fig. S.

? *Rhizochalina singaporensis* Ridley and Dendy, 1887, p. 34.

*Rhizochalina singaporensis* Lindgren, 1897, p. 481.

*Rhizochalina singaporensis* Lindgren, 1898, p. 297, pl. XIX, fig. 11.

*Histoderma singaporensis* Thiele, 1903, p. 955.

*Coelosphaerella vesiculatum* de Laubenfels, 1934, p. 21.

*Coelocarteria singaporense* Burton, 1934, p. 563.

*Ichnodonax kapne* de Laubenfels, 1954, p. 112.

*Ichnodonax singaporensis* Lévi, 1961, p. 518.

OCCURRENCE: Sta. 10, 15, 92.

DISCUSSION: The three specimens from the Palau Islands are identical, except in dimensions, with de Laubenfels' specimens of *Ichnodonax kapne* from the same locality. (The thinner, inhalant fistules are up to 6.5 cm long.)

Dendy (1905), in his description of *Histoderma vesiculatum*, mentioned that palmate isohelae were present in the type of *Phloeodictyon singaporense* Carter. If this fact is considered, then the only difference between *P. singaporense* and *Ichnodonax kapne* de Laubenfels is that the oxaeas are thinner in the latter. Other specimens from the Palaus have slightly



TABLE 5

SPECIMEN	LOCALITY	HABIT	OXEAS	STRONGYLES	ISOCHELAE	FIBRES	COLOR
<i>Phaeodictyon singaporense</i> Carter, 1883	Singapore	incomplete specimen, sub-hemispherical with fistules	$300 \times 17\mu$	$40-80 \times 4\mu$	present (Dendy, 1905)	—	bright yellow in life, brown in dried state
<i>Rhizochalina singaporensis</i> var. Ridley, 1884	Torres Str., 7 fms.	tubular and elongate to barrel shape with fistules on upper surface	$300 \times 12.7\mu$ to $280 \times 4\mu$	present	presumably present (Burton, 1934)	—	chestnut to purplish brown in alcohol
<i>R. singaporensis</i> R. and D., 1887	Tristan da Cunha, 360 fms.	broken fistule only	no details, very doubtfully of the same species				
<i>R. singaporensis</i> Lindgren, 1898	China Sea	oval body with fistule					
<i>Histoderma singaporensis</i> Thiele, 1903	Ternate	oval with fistules	$300 \times 15\mu$	small	$15\mu$	—	brown
* <i>Histoderma vesiculatum</i> Dendy, 1905	Gulf of Manaar, deep water	elongate cylinder inflated at intervals to oval vesicles	$300 \times 9\mu$ variable young forms present	$40-100 \times$ $5-7\mu$ variable	$16\mu$	$165\mu$	pale brown with a purplish tinge
* <i>Ichnodonax kapne</i> de Laubenfels (1954)	Palau Is.	rhizome expanded into vesicles with vertical fistules from upper surface	$262-290 \times$ $5.5-11.5\mu$	$46-112 \times$ $3.5-7\mu$	$14.5-17.5\mu$	$187-312\mu$ (main fibres only)	dark olive to medium yellow in life, red-brown in alcohol
<i>Ichnodonax singaporensis</i> Levi, 1961	Zamboanga	cushion-like with fistules	$240-275 \times$ $6-12\mu$	$30-100 \times$ $5-8\mu$	$14-15\mu$	$250-300\mu$	—
Sta. 10 Palau	Palau	rhizome expanded into vesicles with fistules mainly from upper surface	$260-290 \times$ $10-12\mu$	$50-112 \times$ $4-7\mu$	$14-17.5\mu$	$200-430\mu$ (main fibres only)	brown in life, brown and black in alcohol
Sta. 15 Palau	Palau	identical to Sta. 10	$237-300 \times$ $3.5-13.5\mu$	$50-112 \times$ $3.5-9\mu$	$14-18\mu$	—	golden brown in alcohol, yellowish- green in life

\* The type of *I. kapne* and a spicule mount of the type of *H. vesiculatum* have been examined.



thicker oxeas and Carter gave no range in dimensions for his specimens. Only Carter and de Laubenfels have reported the life color of their specimens; in both cases they were yellow. Examination of a spicule mount of the type of *Histoderma vesiculatum* Dendy (BM 1907.2.1.60) reveals greater variation in the dimensions of the oxeas than reported by Dendy and leaves no doubt that this species is synonymous with *P. singaporense*. Burton (1934) erected the genus *Coelocarteria* for *P. singaporense*. No later authors have used this genus.<sup>8</sup> De Laubenfels (1934) referred *H. vesiculatum* Dendy to *Coelosphærella*, a genus defined as having toxas; he later (1954) erected a new genus, *Ichnodonax*, to receive a Palau sponge, *I. kapne*, which is now considered synonymous with *Coelocarteria singaporense* Carter.

Lévi (1961) considers *H. vesiculatum* Dendy to be a synonym of *P. singaporense*, which he referred to *Ichnodonax* as a species distinct from *I. kapne*. A tabulation of the salient characters recorded by all authors for *C. singaporense* and its synonyms (Table 5) affords little basis for retaining more than a single species, which has a general Indo-Pacific distribution.

**DISTRIBUTION:** Singapore (Carter); Torres St. (Ridley); China Sea (Lindgren); Ternate (Thiele); Ceylon (Dendy); Palau Islands (de Laubenfels); Zamboanga (Lévi).

#### SUBORDER MYXILLIFORMES de Laubenfels

#### FAMILY TEDANIIDAE Ridley and Dendy

#### GENUS *Iotrochota* Ridley

*Iotrochota* Ridley, 1884, p. 433.

*Hiattrochota* de Laubenfels, 1950, p. 19.

#### *Iotrochota baculifera* Ridley

*Iotrochota baculifera* Ridley, 1884, p. 435, pl. XXXIX, fig. M, pl. XLII, fig. F.

*Iotrochota baculifera* Thiele, 1899, p. 18.

*Hiattrochota baculifera* de Laubenfels, 1954, p. 124, fig. 77.

<sup>8</sup>De Laubenfels (1936) states "*Coelocarteria* Burton has many monaxons, that is to say, styles." This is not the case; occasional stylote modifications of oxeote spicules have been reported for *Coelocarteria singaporense*, but styles do not constitute a major proportion of the skeleton.

*Hiattrochota biatti* de Laubenfels, 1954, p. 125, fig. 78.

*Hiattrochota mystile* de Laubenfels, 1954, p. 126, fig. 79.

**OCCURRENCE:** Sta. 236A.

**DESCRIPTION:** Only two tiny specimens are in the Palau collection, both encrusting upon *Clathria fasciculata*; one is intact and has the variable surface features which characterize this species. The color reported by de Laubenfels for *Hiattrochota mystile*, to which this specimen compares most closely, is black in life. In alcohol both the type (USNM 23018) and the Palau specimens are deep purplish-red (R 3/4).

The spicule dimensions conform closely to those of the type of *H. mystile*.

*Megascleres.* Strongyles, 225–255 × 3.5–5.0μ. Styles, 125–180 × 5.5–7.5μ.

*Microscleres.* Birotulae, 13–16.5μ usually with twelve teeth at each end; some appear to have only eight.

**DISCUSSION:** Several specimens of *Iotrochota* have been examined to determine whether the constantly recurring strongyles were localized at the surface; for if this is so, the genus *Hiattrochota* de Laubenfels cannot be maintained. In *I. birotulata* from Jamaica, *I. baculifera* from Bora Bora, the Palau specimens, and the holotype of *Hiattrochota mystile* there is a consistently higher proportion of strongyles to styles in dermal spicule preparations, and, although the pigmentation of these sponges somewhat obscures detail in sections, it appears that all tangential dermal spicules are strongyles.

The type species of *Hiattrochota*, *H. protea* from Hawaii, is probably a synonym of *I. baculifera*; the only features which distinguish it are the massive form and the absence of a well-defined skeleton of spicule tracts. For the present *H. protea* is retained as a separate species of *Iotrochota*. *H. ditrocha* from the Palau Islands also seems sufficiently distinct to remain as a separate species; it is ramose to repent in form and is reported to contain raphides.

The genus *Iotrochota* was grouped by de Laubenfels (1936) with his Desmacidonidae; it is obviously better to regard this genus as a myxillid in which some species (e.g., *I. purpurea*) have lost the ectosomal spicules. This is essen-



FIG. 21a. *Microciona eurypta* (de Laubenfels). Section showing the basal spongin plate with embedded acanthostyles and styles. In the embryo traces of Spongin B are visible.

tially the position Dendy (1921) advocated for *Iotrochota*.

**DISTRIBUTION:** North Australia (Ridley); Celebes (Thiele); Philippines (Lévi); Marshall Islands; Truk (de Laubenfels).

**SUBORDER MICROCIONIFORMES** de Laubenfels

**FAMILY MICROCIONIDAE** Hentschel

**GENUS MICROCIONA** Bowerbank

*Microciona eurypta* (de Laubenfels)

Fig. 21a, b

*Dictyociona eurypta* de Laubenfels, 1954, p. 143, fig. 91.

**OCCURRENCE:** Sta. 220A.

**DESCRIPTION:** This species is an encrustation, 0.5–0.8 mm thick, extending over both surfaces of a shell of *Chama* sp.

**COLOR:** In alcohol, pale brown, between (yY-R 8/4) and (yY-R 7/4).

**SURFACE:** Macroscopically smooth, granular, and minutely hispid under low magnification; no pores or oscules are visible. The dermal membrane is skin-like and packed with small subtylostyles.

**SKELETON:** A basal plate of spongin, 10–15  $\mu$  thick, supports vertically disposed acanthostyles. Long styles, either singly or in brushes, also diverge from this spongin plate in which they are embedded. Between adjacent spicule brushes

interstitial styles are abundant, many disposed parallel to the substrate. The styles from the basal spicule brushes extend throughout two-thirds of the thickness of the sponge; secondary brushes often arise obliquely from them and extend into the densely packed zone of ectosomal subtylostyles. The latter are arranged in brushes with heads inward, but the concentration of spicules, of both ectosomal and endosomal type, obscures the skeletal arrangement in the superficial regions of the sponge. The zone of ectosomal spicules is 100–125  $\mu$  deep, the external diameter of the spicule brushes is 100–130  $\mu$ .

There is scant development in this species of vertical columns of spongin; small localized thickenings of the spongin base do occur, however. In terms of Lévi's (1960) work upon the skeleton of the Clathriidae, this is a leptocionid state.

**SPICULES:** *Megascleres*. (i) Long, thin subtylostyles, often with asymmetric heads, slightly curved or straight, never spined; 237–490  $\times$  7.5–13  $\mu$ .

(ii) Short, slender ectosomal subtylostyles with microspined, often asymmetric heads; 112–200  $\times$  3.5–5.0  $\mu$ .

The smaller subtylostyles of the first category are those which occur in the endosome with no specific orientation. It is difficult to separate these spicules from the larger dermal subtylostyles except that the latter are always terminally microspined.

(iii) Short, accessory acanthostyles, evenly covered with slightly recurved spines; 80–106  $\times$  4.0–6.5  $\mu$  (including spines up to 13.5  $\mu$ ). Some extremely small acanthostyles, up to 16–25  $\mu$ , are present; these are probably developmental stages.

*Microscleres*. (i) Palmate isochelae of two distinct size groups: large, 13.5–18  $\mu$ ; small, 3.5–5.0  $\mu$ .

(ii) Toxa of considerable size range, the larger tending to be very slightly flexed and resembling raphides, the smaller moderately curved with slightly reflexed tips; 36–181  $\mu$  (86  $\mu$ ) and less than 1.0  $\mu$  in diameter.

The sponge contains embryos at a late stage of segmentation; these are localized just above the spongin base and occupy approximately half

the thickness of the sponge. Short tracts of spongin have developed inside the embryonic tissue (Fig. 21a).

DISCUSSION: This species is very closely comparable with *Microciona maunaloa* de Laubenfels from Hawaii, the two, insofar as can be determined, being the only species of *Microciona* having extremely small isochelae as a third microscelere category.

Sufficient small differences exist between the two species to allow the Palau specimen to remain as a separate species.

The size and shape of the acanthostyles, the shape of the larger subtylostyles, and slight size differences in the microscleres are the only divergent characters in the spiculation of the two species. The Palau specimen, however, does not show the color change to blue on fixation that

de Laubenfels reports for *M. maunaloa*, and its color in life is pale brown.

De Laubenfels (1954) described *M. eurypa* as a *Dictyociona*, presumably placing emphasis upon the slight spination of many of the styles. Topsent (1913) differentiated *Dictyociona* from *Microciona* by the presence in the former of a spicule fibre network rather than a series of independent plumose columns. *Microciona eurypa* possesses neither spined main megascleres nor a network of spicule fibres.

DISTRIBUTION: Palau Islands (de Laubenfels).

GENUS *Clathria* Schmidt

*Clathria cervicornis* (Thiele)

Fig. 14iv

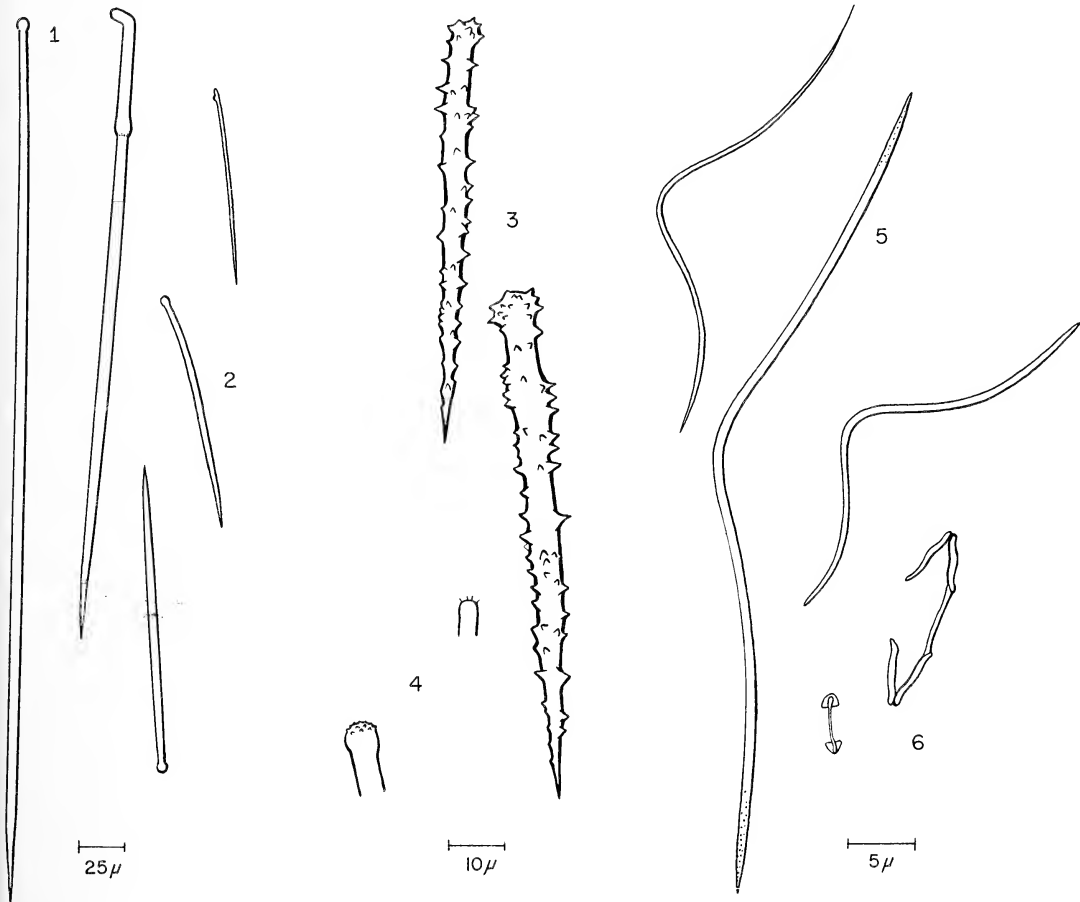


FIG. 21b. *Microciona eurypa* (de Laubenfels). Spicules: 1, Large styles. 2, Auxiliary subtylostyles. 3, Acanthostyles. 4, Ends of auxiliary subtylostyles. 5, Toxa. 6, Isochelae.

TABLE 6

CHARACTERISTICS	<i>M. maunaloa</i>	<i>M. eurypa</i>
Large styles	425 × 13μ (and up)	287-490 × 7.5-13μ
Ectosomal styles	120-160 × 6μ (scattered spicules 240 × 9μ)	112-237 × 3.5-5μ
Acanthostyles	42 × 8μ	80-106 × 4-6.5μ
Large isochelae	14μ	13.5-18μ
Small isochelae	5-6μ	3.5-5μ
Toxa	56-132μ	36-181μ
Color in life	caramel-brown	coffee

*Rhaphidophlus cervicornis* Thiele, 1903, p. 959, pl. 28, fig. 24.

*Rhaphidophlus cervicornis* Brøndsted, 1934, p. 22.

*Thalysias cervicornis* de Laubenfels, 1954, p. 135, fig. 86.

OCCURRENCE: Sta. 220B.

DESCRIPTION: Several fragments of this sponge were collected and all are probably part of one colony. The habit is ramose, with irregularly disposed branches, 0.7-1.0 cm in diameter, in many cases reduced to short nodules, arising from a repent base which produces numerous short processes at right angles to its long axis.

COLOR: In alcohol, pale brown to gray (Y-RY 7/2) to (Y-R-Y 7/5) for the ectosome, mid-brown for the endosome (yY-R 4/4).

TEXTURE: The ectosome is soft and easily torn; the endosome is stiff and incompressible.

SURFACE: Macroscopically smooth, marked by ramifying subdermal canals. Under low magnification numerous dermal spicule tufts are visible and render the surface minutely hispid. Only two oscules are visible, 0.5 and 0.8 mm in diameter, situated on the main stem at the junction of a branch.

SKELETON: The spiculation and the arrangement of the skeleton are entirely typical of *Rhaphidophlus* as redefined by Lévi (1960). A compact, fibrous endosome of plumoreticulate pattern is invested by an ectosome of comparatively fleshy nature supported by special ectosomal spicule brushes which are most pronounced in the subdermal position.

The endosomal fibres are cored in their central third by smooth subtylostyles often having asymmetric heads. Short acanthostyles echinate the fibres. Interstitial subtylostyles are abundant and are in no way distinct from the coring spicules or from the bulk of the ectosomal spicules. The subtylostyles making up the surface brushes tend to be finer and smaller than the interstitial spicules.

Endosomal spongin fibres are 70-350μ in diameter, with frequent anastomoses and little soft tissue remaining between them. The ectosome is 0.1-0.2 cm wide, supported chiefly by obliquely disposed bundles of subtylostyles and, at intervals, by short lateral branches from the endosomal fibres. These fibres never extend to the surface of the sponge. In the superficial region of the ectosome the spicules are of a slightly different type, grouped into brushes oriented at right angles to the sponge surface. These dermal brushes arise from a region 125-300μ below the sponge surface and fan out externally to a diameter of 200-350μ. Between the bases of the brushes is a zone of subdermal cavities overlain by the dermal membrane.

SPICULES: *Megascleres*. (i) Coring and interstitial subtylostyles, slender, slightly wavy or curved in the proximal third, with frequently asymmetric heads; 262-325 × 4.5-6.0μ (291 × 5.0μ).

(ii) Echinating acanthostyles, often with subtylote heads and clear of spines in the proximal half of the shaft; 50-62 × 4.5-6.5μ (57 × 5.7μ).

(iii) Auxiliary dermal subtylostyles; 95-132 × 3.0-4.5μ (109 × 3.8μ).

*Microscleres*. (i) Palmate isochelae, 8.0–13.5 $\mu$  (12 $\mu$ ).

(ii) Toxa; 40–50 $\mu$  once flexed, steepness of flexure variable; not abundant.

EMBRYOS: Pale orange pigmented embryos (Y-R 6/4) are situated at the ectosome-endosome junction and are particularly abundant in the more superficial ectosomal region in the vicinity of oscules. The embryos are 250–300 $\mu$  in diameter, somewhat discoid, and contain abundant fine subtylostyles.

DISCUSSION: This specimen is comparable in detail with de Laubenfels' specimen of *R. cervicornis* from the Marshall Islands. De Laubenfels describes the "microvelvet" surface attributable to the presence of projecting brushes of dermal spicules but makes no further mention of the dermal skeleton or of the spicules which constitute it. Spicule measurements differ only slightly from those given by Thiele (1903).

DISTRIBUTION: Ternate (Thiele); East Indies (Brøndsted); Marshall Islands (de Laubenfels).

*Clathria fasciculata* Wilson

*Clathria fasciculata* Wilson 1925, p. 442, pl. 42, fig. 6, pl. 49, fig. 7, 8.

*Clathria fasciculata* de Laubenfels, 1954, p. 140, fig. 89.

OCCURRENCE: Sta. 220A, 236A.

DESCRIPTION (Table 7): The two specimens are erect, ramose or incipiently so.

COLOR: In alcohol, pale red-brown, near (y4-R 7/4).

TEXTURE: Tough and elastic.

SURFACE: Uniformly conulose. The shape of the conules varies from rounded to pointed and in one specimen they tend to be aligned in verti-

cal rows. The dermis appears granular and, in places where dermal spicule tufts are developed, is slightly hispid; this is more evident at the apex of conules than elsewhere. No oscules are apparent; pores are visible between the conules and above subdermal cavities where the dermal membrane is thinnest.

SKELETON: The characteristic feature of this species is the presence of fasciculate ascending fibres cored by styles. Between these fasciculate columns, which are 300–750 $\mu$  in diameter (individual fibres 75–150 $\mu$ ), is a dense and irregular reticulum of secondary fibres. External to the fibres auxiliary styles are abundant. In the endosome these have no regular arrangement; in the ectosome they are obliquely or tangentially disposed or, in places, organized to form dermal brushes. Echinating acanthostyles are present on all fibres, usually occurring singly, but sometimes in tufts at the nodes.

The ectosome is a cavernous layer varying from 250–900 $\mu$  in thickness, according to the size of the subdermal cavities at any given point. Thin obliquely oriented tracts of auxiliary styles run across the ectosome between subdermal cavities. The main spicule concentration in this region is in the tangential spicules and dermal brushes situated in the dermal membrane.

SPICULES: *Megascleres*. (i) Smooth styles, slightly curved, coring the endosomal fibres; 162–250  $\times$  5.5–11 $\mu$  (200  $\times$  7.5 $\mu$ ).

(ii) Slender straight auxiliary styles occurring throughout the sponge except in the fibres; 100–270  $\times$  2.5–6.6 $\mu$  (200  $\times$  4 $\mu$ ).

(iii) Echinating acanthostyles, short, slightly tylote with spines concentrated on the head and distal half of the shaft; 50–62.5  $\times$  5–7 $\mu$  (58  $\times$  6.25 $\mu$ ).

TABLE 7

SPECIMEN	HEIGHT	WIDTH	LENGTH OF BRANCHES	BRANCHES	SHAPES OF CONULES	HEIGHT AND SPACING OF CONULES
Sta. 220A	4.5 cm	5.0 cm	—	stem 3.0 cm	rounded or sharp pointed	0.4–3.0 mm high 2.0–4.5 mm apart
Sta. 236A	6.5 cm	0.7–1.0 cm	1.5 cm	stem 0.7–1.0 cm	sharp	0.5–3.0 mm high 2.0–6.0 mm apart

*Microcleres*. (i) Palmate isochelae, 8.0–14.5 $\mu$  (12.25 $\mu$ ).

(ii) Toxa of considerable range of size and shape, the smaller being tricurvate, the larger approaching raphides, very little flexed, and occasionally completely straight, rare; 33–137 $\mu$  (75 $\mu$ ).

DISCUSSION: This species, both as described by Wilson (1925) and as represented in the Palau collection, is intermediate between *Clathria* Schmidt and *Rhaphidophlus* Ehlers in the features of the dermis. Lévi (1960) redefined and maintained both genera, laying considerable stress on the tufted arrangement of the dermal spicules in *Rhaphidophlus* as opposed to the irregular, oblique to tangential arrangement in *Clathria*. The configuration of the dermal spicules varies from place to place in *Clathria fasciculata*. *Microciona eurypta* has almost as well-developed a system of dermal brushes as has a typical *Rhaphidophlus*, and many other examples of this type of dermal specialization can be cited in *Microciona* in conjunction with the nonplumose skeleton which to a great degree characterizes the genus. It is difficult to differentiate clearly between *Microciona* and *Clathria* on the basis of the form of the skeleton because of the existence of such intermediate forms as *Microciona prolifera*; clearly, the dermal skeleton is too variable to be of sys-

tematic importance. For the latter reason *Rhaphidophlus* is not maintained as a genus distinct from *Clathria*. The question of the possible synonymy of *Microciona* and *Clathria* is not considered here since only detailed study of large collections and type material will suffice to resolve it.

It appears from the material in this collection that a firmer basis for the generic separation of *Rhaphidophlus* would be to stress the great axial condensation with sharply demarcated ectosomal and endosomal regions, rather than the notoriously variable dermal skeleton.

DISTRIBUTION: Philippines (Wilson); Palau Islands; Truk (de Laubenfels).

#### FAMILY OPHLITASPONGIIDAE de Laubenfels

##### GENUS *Mycale* Gray

##### *Mycale lissochela* n. sp.

Fig. 22a, b

OCCURRENCE: Sta. 220 (Holotype, USNM 23702), 220A (Paratype, USNM 23701).

DESCRIPTION: Both specimens of this species are thickly encrusting, in one case over a hydroid, in the other over a coral fragment. In specimen 220A the sponge contains many small zoanthids and around each of these the sponge dermis is raised in a membranous chimney. These do not appear to be the oscules, since groups of smaller openings lying flush with the sponge surface are common.

DIMENSIONS (TABLE 8).

COLOR: In alcohol, pinkish-gray (220A) (Y-R 7/2) to (rY 8/4) pale creamy yellow (220).

TEXTURE: Extremely soft and very slightly elastic.

SURFACE: Smooth, and the dermis is variable in structure. In specimen 220A the fleshy tissues of the dermis are arranged so as to form a reticulate pattern; in the other specimen this pattern is only faintly discernible in isolated areas. For the most part the fleshy tissues are uniformly dispersed, and no pores or oscules are visible.

SKELETON: Composed of thin curving sparsely branched tracts composed of subtylostyles. Immediately below the surface the larger tracts break up into three or more divergent

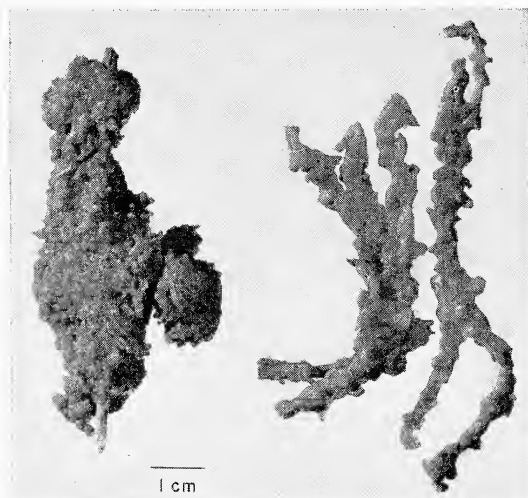


FIG. 22a. *Mycale lissochela* n. sp. Left, Sta. 220A. USNM 23701; right, Sta. 220. Holotype. USNM 23702.

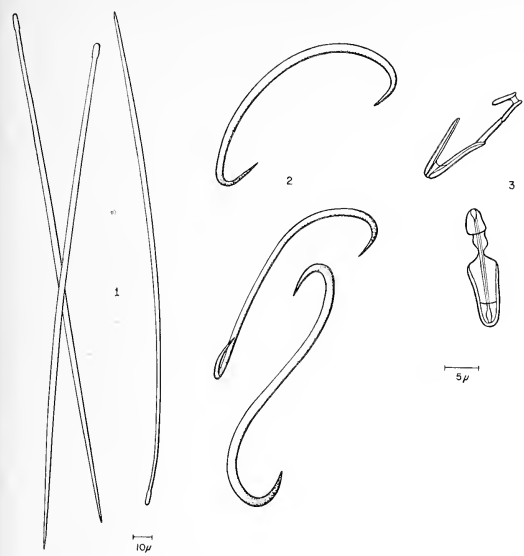


FIG. 22*b*. *Mycale lissochela* n. sp. Spicules: 1, Subtylostyles. 2, Sigmas. 3, Palmate anisochelae.

branches. Interstitial megascleres are abundant throughout the sponge and occur tangentially disposed in the dermal membrane. Microscleres, sigmas, and isochelae, occur throughout the sponge; sigmas are particularly abundant in the dermis.

Fibres range from 10–75µ in diameter. The construction of the sponge is relatively compact; there is no development of huge subdermal or interfibrillar spaces as in many mycalids.

SPICULES: *Megascleres*. Subtylostyles, straight or very slightly curved with elongate oval heads; 212–275 (252) × 3.0–4.5µ (3.6µ).

*Microscleres*. (i) Sigmas, C-shaped with sharply reflexed tips, which are frequently in different planes; occasional S-forms occur. These spicules are abundant throughout the flesh and

in the dermal membrane; 19–40µ (33.9µ). (ii) Palmate anisochelae, small spicules with thin alae; 3.0–3.5µ wide, 13–20µ (16.2µ) long.

DISCUSSION: Burton (1956) has drawn attention to a group of species within *Mycale* which have in common (a) small narrow anisochelae<sup>9</sup> of one size group only, (b) a single category of sigmas which are approximately twice the size of the chelae, (c) tylostyles or subtylostyles between 200–300µ. To this list of characters Burton adds a fourth, “the spiculation of Topsent’s subgenus *Carmia*.” This statement is quite misleading, as none of the species Burton then proceeds to list has the spiculation of *Carmia*.

*Mycale lissochela* is extremely close in spiculation and structure to *Mycale cecilia* de Laubenfels, *M. microsigmatosa* Arndt, *Mycale senegalense* Lévi, and *M. phyllophila* Hentschel, and is comparable to *M. angulosa* (D. and M.), *M. fistulata* Hentschel, *M. serpens* (Lendenfeld), and *M. tenuispiculata* (Dendy). The last four species, however, are massive rather than encrusting.

*Mycale angulosa* is comparatively well known; it has a distinctive habit, cavernous architecture, and rare microscleres. Thus, despite close similarity in spiculation to the other species mentioned it can certainly be maintained as a separate species. *Mycale cecilia* cannot be distinguished from *M. microsigmatosa* and the latter can only be considered distinct from *M. phyllophila* Hentschel on the grounds of distribution. Lévi (1959) has already indicated that his *M. senegalense* is probably synonymous with *M. microsigmatosa* Arndt. *M. maunakea* de

<sup>9</sup> Burton’s text reads “isochelae,” which I have interpreted as a misstatement; it is confusing, however, as some species of *Mycale* are reported to have isochelae.

TABLE 8

SPECIMEN	THICKNESS (cm)	LENGTH (cm)	WIDTH (cm)	OSCULES (mm)
Sta. 220	0.2–0.35	broken	—	not apparent
Sta. 220A	0.3–1.1	7.5	1.5–3.5	0.4–0.6



TABLE 9

SPECIES	MEGASCLERES	SIGMAS	ANISOCHELAE	HABIT	COLOR
<i>Mycale cecilia</i> Panama de L., 1936	tylostyles 300 × 7–10μ	30μ	22–25μ 12–15μ narrow alae	encrusting	green with red embryos
<i>Mycale cecilia</i> Hawaii de L., 1950	long headed tylostyles figure indicates styles 240–250 × 4–6μ	30–42μ	15–24μ no mention of 2 categories, narrow	encrusting	variable
<i>Mycale maunakea</i> Hawaii de L., 1951	tylostyles 160–240 × 2–6μ (210 × 5μ)	37–42μ	13–22μ	encrusting	pale pink
<i>Mycale senegalense</i> Lévi	subtylostyles ovoid heads 220–280 × ?	30–40μ	20–22μ	encrusting	gray-red
<i>Mycale phyllophila</i> Hentschel, 1911, Australia	tylostyles to subtylostyles 206–259 × 4–5μ	31–40μ	19–20μ (6μ across) 11–12μ (4μ across)	encrusting	
<i>Mycale fistulata</i> Hentschel, Australia	subtylostyles 248–296 × 3–4μ	42–65μ	24–26 × 7–9μ	encrusting to erect 15 cm	
<i>M. fistulata</i> var. <i>micro-</i> <i>sigmatosa</i> Arndt, 1927, Curaçao	subtylostyles 250–294 × 3μ	32–38μ	8–19μ	encrusting	
<i>Mycale lissochela</i> Palau Is.	subtylostyles	19–40μ	13–20μ	encrusting	

Laubenfels is distinctive only in the possession of a completely non-reticulate skeleton.

*Mycale lissochela* differs from other species in this group in having tangential megascleres in the dermis, not regularly arranged but certainly representing a dermal skeleton. This species is closest to *M. phyllophila* Hentschel; the chief difference between the two is in the spiculation of the epidermis, which consists of irregularly strewn megascleres in *M. lissochela* and of microscleres only in Hentschel's species. In the absence of large population samples it is difficult to evaluate the significance of this difference. In view of the emphasis placed on the morphology of the dermis in the systematics of the genus *Mycale*, it is preferable to note the differences rather than to ignore them by synonymizing the two species.

There are other species mentioned by Burton as being part of this group; of these *Mycale euplectelloides* Row, *M. regularis* Wilson, and

*M. imperfecta* Baer have much larger sigmas and have a fibroreticulate skeleton, and *Mycale fistulifera* Row has a distinct lobate habit. *Mycale mytilorum* Annadale may belong to this group, but this reference cannot be verified.

*Mycale (Aegagrophila) cavernosa* n. sp.

Fig. 23a, b, c

OCCURRENCE: Sta. 125 (a single specimen which is designated Holotype, USNM 23703).

DESCRIPTION: Two fragments of this sponge were obtained; it appears to have grown upright from a broad base of attachment. The fragments are lobate, much folded, and give the impression of having shrunk and distorted considerably after fixation; both contain large quantities of fine debris. Dimensions are 5 cm high, 20 cm wide, 1.5 cm thick; and 5 cm high, 2.5 cm wide, 0.7 cm thick.

COLOR: In alcohol, is grayish-white.

TEXTURE: The sponge is soft but slightly elastic.

**SURFACE:** Deeply folded and raised into mounds. The dermal membrane is  $60\text{--}125\mu$  thick, and contains a more or less regular spicule reticulum and large quantities of fine calcareous debris. Projecting spicules from the subdermal brushes render the surface slightly hispid.

Small oscular areas are dispersed irregularly over the surface, each giving access to a large subdermal cavity. Circular and oval pores are evenly scattered over the entire dermal membrane and range from  $62\text{--}100\mu$  in diameter.

**SKELETON:** The dermal skeleton is made up of a series of intersecting fibres varying from 1–8 spicules wide ( $4.5\text{--}38\mu$ ) and delimiting roughly triangular meshes,  $62\text{--}375\mu$  across. In addition to the megasclere skeleton, the dermis contains isolated anisochelae, usually of the smaller category. Immediately beneath the dermal membrane are huge subdermal cavities

which extend deep into the interior of the sponge. The primary fibres of the endosome are stout, sparsely branched, and invested with spongin, which is just visible as a thin clear zone external to the spicules along the fibre, but which is more abundant at the intersection of branches. A weak system of secondary fibres is present but does not form a coherent reticulum; the over-all aspect of the skeleton is lax, with considerable emphasis on the interstitial material, both spicules and calcareous debris.

Primary fibres range from  $90\text{--}185\mu$  ( $135\mu$ ) in diameter; secondary fibres,  $25\text{--}100\mu$  ( $62\mu$ ). At intervals the dermal membrane is supported by radiating spicule brushes,  $20\text{--}50\mu$  wide, usually occurring in groups of 3–5. These are united by spongin to the nodes of the dermal skeleton. These spicule brushes arise from the



FIG. 23a. *Mycale cavernosa* n. sp. Sta. 125. Holotype. USNM 23703.

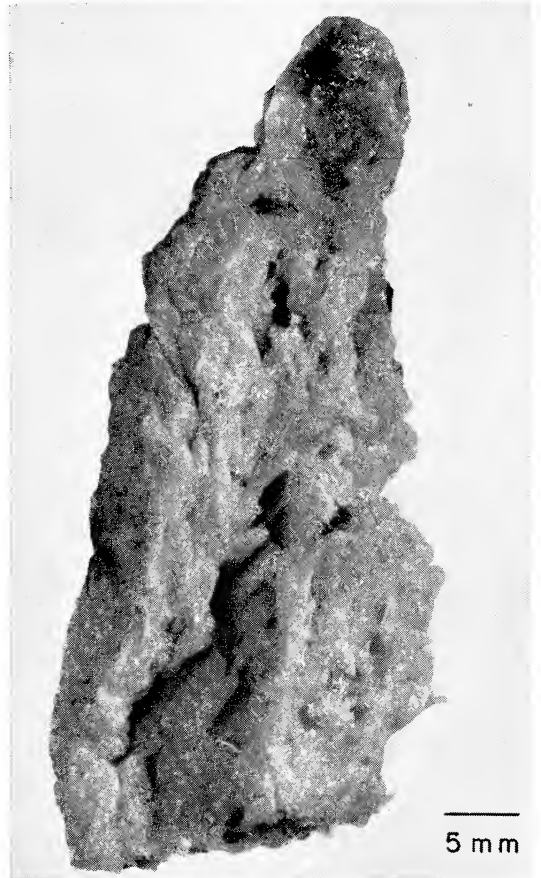


FIG. 23b. *Mycale cavernosa* n. sp. Sta. 125. Holotype. USNM 23703.

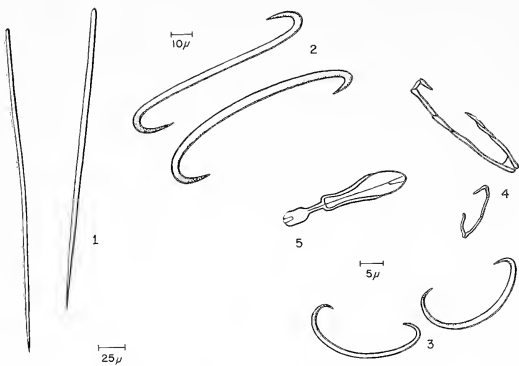


FIG. 23c. *Mycale cavernosa* n. sp. Spicules: 1, Subtylostyles. 2, Large sigmas. 3, Small sigmas. 4, Anisochelae. 5, Anisochela, face view.

secondary fibres which run at an acute angle to the surface of the sponge. Often the primary fibres run without branching to the surface. The details of branching and interrelations of the three orders of endosomal fibres are very difficult to clarify owing to the excessive amounts of foreign matter present.

**SPICULES:** *Megascleres*. Smooth, often slightly wavy or curved styles with a slight constriction of the shaft behind the head. The finer styles tend to be interstitial, the stouter spicules are contained in fibres;  $262\text{--}351 \times 0.8\text{--}8\mu$  ( $306 \times 4.2\mu$ ).

*Microscleres*. (a) Sigmas, of two size groups: (i) large stout C- or S-shaped sigmas with strongly reflexed tips;  $92\text{--}105 \times 1.5\text{--}5\mu$  ( $97.5 \times 3.6\mu$ ), and (ii) small abundant C-shaped sigmas with sharply reflexed tips and one end rotated;  $19\text{--}26.5\mu$  ( $23\mu$ ).

(b) Palmate anisochelae of two size groups, never arranged in rosettes: (i) larger, often with acutely recurved alae, the latter one-half to two-thirds the length of the shaft;  $29\text{--}40\mu$

( $33\mu$ ), and (ii) smaller, extremely abundant with acutely recurved alae, rarely more than half the length of the shaft;  $11\text{--}15\mu$  ( $13.5\mu$ ).

**HISTOLOGY:** Soft tissue is much reduced in this sponge except in the dermis, and the structure and disposition of such tissues is masked by incorporated debris.

**DISCUSSION:** *Mycale cavernosa* falls clearly into Topsent's subgenus *Aegrophila* since it possesses a dermal reticulation of spicule fibres. It differs from all other members of this subgenus in the combination of a relatively regular dermal skeleton with comparatively small fine megascleres supplemented by extremely large sigmas.

GENUS *Neofolitispa* nom. nov.

*Neofolitispa dianchora* (de Laubenfels)

Fig. 24a, b

*Monanchora dianchora* de Laubenfels, 1935, p. 331, pl. 1, fig. 4.

*Foliispa pingens* de Laubenfels, 1954, p. 159, fig. 104.

*Monanchora clathrata* Lévi, 1961, p. 135, fig. 8.

**OCCURRENCE:** Sta. 59, 92, 100.

**DESCRIPTION:** Two specimens are erect, lobate to massive; the third is encrusting with occasional low processes.

**DIMENSIONS** (Table 10).

**COLOR:** In life, scarlet; in alcohol, externally from pale fawn (Y-R-Y 8/2–Y-R-Y 8/4) to greenish-yellow (Y 5/4) and pale brown (R-Y-R 6/4) merging into greenish-yellow. Interior, pale yellow-green (Y 7/4).

**TEXTURE:** Compressible but tough; somewhat slimy.

**SURFACE:** Irregularly lumpy, the dermal

TABLE 10

SPECIMEN	HEIGHT (cm)	WIDTH (cm)	THICKNESS (cm)	SURFACE PROCESSES (mm)
Sta. 59	4.5	2.0	1.2	up to 1.0
Sta. 92 encrusting	—	7.0–6.5	—	up to 11
Sta. 100	4.0–6.5	9.5	3.5	1.5–6.0

membrane smooth and skinlike, slightly granular to hispid in patches. In two specimens (Sta. 92 and 59) the pores have remained open over most of the surface and under low magnification give the sponge a regular lacy appearance. At irregular intervals the pore reticulation of the dermal membrane overlies deep subdermal cavities; there is no differentiation of the membrane at such points, but they presumably represent oscular sieves, 0.8–2.0 mm in diameter.

**SKELETON:** The ectosomal skeleton is composed principally of brushes of subtylostyles arising from the endosomal fibres and spreading tangentially into the dermal membrane. In addition to these tangential megascleres, which are never abundant, the dermal membrane contains great numbers of isochelae predominantly of the larger category.

The endosomal skeleton is a system of plumose fibres cored by subtylostyles invested by

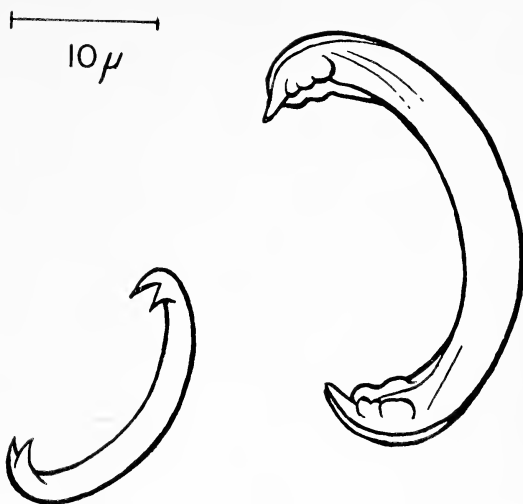


FIG. 24b. *Neofolitispa dianchora* (de Laubenfels). Isochelae.

spongion, in the deeper regions of the sponge losing most of the spongion and narrowing to the point below the surface where they break up into subdermal brushes.

In addition to the ectosomal and endosomal fibres, there are abundant interstitial spicules which, in the encrusting specimen, predominate over the spicules arranged in fibres. This gives the skeleton a somewhat confused aspect, but the incipient plumose structure is still discernible. The specimen from Sta. 92 closely approximates the holotype of *Folitispa pingens* (USNM 22924) in features of the skeleton. The dermal concentration of isochelae is present in the type, although not mentioned by de Laubenfels, and there are some tangential dermal megascleres in addition to the subdermal spicule brushes. In neither the Palau specimens nor the type is there any localization of distinct megasclere categories or any occurrence of echinating spicules.

Fibre dimensions are variable, up to  $380\mu$  in diameter in the center of the sponge, narrowing to approximately  $125\mu$  at the point where the subdermal spicule brushes arise.

**SPICULES:** *Megascleres.* Straight subtylostyles often stair-stepped terminally or occasionally modified to tylostrongyles. Some spicules are true tylostyles with irregular heads;  $262\text{--}360 \times 3.5\text{--}8.0\mu$  ( $342\text{--}6.0\mu$ ).



FIG. 24a. *Neofolitispa dianchora* (de Laubenfels). Sta. 59.

*Microscleres*. Unguiferate anchorate isochelae of two sizes: (a) large, strongly-curved chelae with thick shaft, slightly expanded at each end, the expansions bordered by four sharp triangular teeth;  $27-34 \times 3.6-4.2\mu$  ( $29.5 \times 4.0\mu$ ), and (b) small, fine, almost C-shaped chelae with three sharp teeth at each end; the two lateral teeth are often directed almost at right angles to the shaft, while the central tooth continues the axis of the shaft;  $6.5-20 \times 1.0\mu$  approximately.

REPRODUCTIVE STAGES: Eggs and embryos are present in one specimen and in the holotype. The embryos contain numerous very fine megascleres but apparently no microscleres. They are ovoid, approximately  $375 \times 500\mu$ ; cellular detail is not discernible.

DISCUSSION: De Laubenfels (1935) added a species, *M. dianchora*, to *Monanchora* Carter which, up to that time contained only the type species, *Monanchora clathrata*<sup>10</sup>, a poorly known species described from a single wave-worn Australian specimen. *Monanchora dianchora* does not resemble Carter's species at all closely but is identical to *Folitispa pingens* described by de Laubenfels (1954) from the central Pacific.

*Folitispa* was erected by de Laubenfels (1936) for *Hymedesmia laevis* Dendy. This sponge has small dermal tylostyles in brushes, tangential spicules in the dermal membrane, in addition to large endosomal tylostyles and peculiar isochelae of one category only, differing from those of *M. dianchora* in being slightly spathulate isancorae rather than unguiferate isancorae.

Only two species other than the type (*H. laevis*) have been described in *Folitispa*: *F. pingens* (= *M. dianchora*) and *Folitispa acuata* Lévi (1958). Both of these have unguiferate isancorae of two size groups in addition to tylostyles which, in *F. acuata*, are divisible into two size groups; in *F. dianchora*, although there is a special arrangement of dermal megascleres, there is no size differentiation of these spicules. Lévi (1958) pointed out that de Laubenfels, in describing *Folitispa pingens*,

had added a species to *Folitispa* which did not conform to the characters of the type, there being no megasclere differentiation and the skeleton being confused. Restudy of the type of *F. pingens* shows that a plumose skeletal arrangement is present, although feebly developed owing to the encrusting form. It is important to note that the form of the isochelae is different in the type species, *H. laevis* (isancorae spathuliferae) and the two later species (isancorae unguiferae). Since this genus is defined principally on chela-type it is difficult to reconcile these two groups in *Folitispa* as it is presently defined.

Lévi mentions *Amphilectus unguiculatus* Dendy as being close to the *Folitispa* group. De Laubenfels (1936) made this sponge the type of *Okadaia*, a new genus possessing "tylostyles and strap-like sigmas with toothed ends." In 1949 de Laubenfels noted that *Okadaia* was preoccupied and replaced this name with *Neosperiopsis* and stated "the diagnosis remains the same." In the same work, however, he named *Neosperiopsis deichmannae* as the type species. *Neosperiopsis deichmannae* is in no way related to *Amphilectus unguiculatus*, the type of *Okadaia*. Hartman (1958) has shown that the microscleres of *N. deichmannae* are perfectly normal isochelae of the "*Homoedictya*" type and that the species is almost indistinguishable from *Isodictya palmata* Bowerbank. *Neosperiopsis* thus falls to *Isodictya*. It should be pointed out that *Okadaia* was initially founded upon a misreading of Dendy's description of *Amphilectus unguiculatus*. Dendy clearly stated that this species possesses isochelae (not sigmas, as de Laubenfels states); further, these chelae are unguiferate isancorae.

There are several points in common between *Amphilectus unguiculatus* and *Folitispa dianchora*: semi-plumose structure, no size differentiation of the megascleres, occasional mucronate or strongylote modification of the tips of the megascleres, spicule size, and chela type. The greatest differences between them are the lack of any dermal megascleres in *A. unguiculatus*, and absence of the small isochelae.

In summary, *Folitispa dianchora* and *Folitispa acuata* are very closely related species which can not be generically linked with *Hy-*

<sup>10</sup> *M. clathrata* has one type of microscle, 5-anchorate with long points ( $8-29\mu$  overall dimensions), subtylote megascleres ( $393 \times 10\mu$ ); surface characters unknown, shape unknown.



FIG. 25. *Pseudaxinyssa pitys* de Laubenfels. Sta. 92.

*medesmia laevis* is the type of *Folitista*. The name *Neofolitista* is proposed here to receive them. *Amphilectus unguiculatus* is certainly very close to *Neofolitista*, but without reference to type material it cannot be placed in the genus. Probably *Esperiopsis viridis* Kieschnick should be included in *Neofolitista*, but this cannot be verified from the literature.

*Monanchora* Carter is retained for *M. clathrata*, a poorly known Australian sponge which Lévi (1961) has incorrectly recorded from the Philippines.

DISTRIBUTION: Puerto Galera, Philippines (de Laubenfels); Palau Islands, Marshall Islands (de Laubenfels).

#### GENUS *Desmacella* Schmidt

*Desmacella lampra* de Laubenfels

*Desmacella lampra* de Laubenfels, 1954, p. 150, fig. 98.

OCCURRENCE: Sta. 104.

REMARKS: This sponge is encrusting to a thickness of 1.2 mm over a specimen of *Teleso* and in the fragment collected shows no tendency to become massive. The color in alcohol is salmon pink (RY-R 6/8). The holotype (USNM 23088) has an identical external color

in alcohol. The dermal membrane contains tangential megascleres, and rare sigmas.

DISTRIBUTION: Marshall Islands (de Laubenfels).

#### ORDER HALICHONDRIDA Topsent

#### FAMILY AXINELLIDAE Ridley and Dendy

#### GENUS *Pseudaxinyssa* Burton

*Pseudaxinyssa pitys* de Laubenfels

Fig. 25

*Pseudaxinyssa pitys* de Laubenfels, 1954, p. 178, fig. 117.

OCCURRENCE: Sta. 92A, Sta. 140 (fragments only).

REMARKS: This specimen is from the same location as the holotype (USNM 23103 and Bishop Museum 137) and is closely comparable with it in size and structure. The spiculation of both the type and the present specimen includes styles and occasional strongyles as modifications of the oxeas.

SPICULES: Oxeas;  $612-812 \times 5-16\mu$ . The holotype shows a corresponding range of spicule size.

DISTRIBUTION: Palau Islands (de Laubenfels).

#### GENUS *Phycopsis* Carter

*Phycopsis* sp. cf. *terpnis* de Laubenfels

*Phycopsis terpnis* de Laubenfels, 1954, p. 176, fig. 116.

OCCURRENCE: Sta. 220A.

DESCRIPTION: A massive, cake-shaped sponge, 13 cm in diameter, 6.5 cm thick. Prominent circular oscules, 0.8–1.0 cm in diameter, are scattered over the upper surface. Each osculum is surrounded by a low collar, 0.4–0.8 cm high with walls 0.8–2.5 mm thick. In all cases the osculum functions somewhat as an exhalant cloaca, receiving 3–12 small exhalant openings about 1.0 cm below the sponge surface.

COLOR: In alcohol, white.

TEXTURE: Crisp and brittle.

SURFACE: Uneven, hispid.

SKELETON: A confused mass of oxeas,  $670-1100 \times 8-22\mu$  ( $877 \times 15.5\mu$ ). The structure

of ectosome and endosome is cavernous, the former having slightly denser protoplasmic matrix than the endosome in which no cellular material remains in this specimen. Small patches of spongin occur binding groups of 2-3 spicules either at their tips or along their axes.

**DISCUSSION:** The poor preservation of this specimen renders it useless for the purpose of close comparison with the type specimen of *Phycopsis terpnis*. The holotype of *Phycopsis terpnis* (USNM 23061) is, unfortunately, only a small portion of the sponge and its spiculation does not compare in detail with that figured by de Laubenfels in the type description. All the stout spicules of this specimen are strongyles,  $600-875\mu \times 19-24\mu$  ( $692 \times 20\mu$ ), which narrow very abruptly to relatively thin, rounded tips. The finer spicules are typical, evenly tapered oxeas,  $700-880 \times 7-15\mu$  ( $793 \times 9.5\mu$ ), as figured. It seems clear that in the holotype there are, indeed, two megasclere categories.

The present specimen is referred to this species since it compares well with the type

description, the main difference being the possession of slightly larger oxeas. It is possible that the holotype has been wrongly labelled or, should this not be the case, that it is equivalent to the Palau specimen and merely has the stouter spicules modified to strongyles. If the latter were true, one would expect styles and occasional oxeas to occur, but such spicules cannot be located in the holotype nor are there any styles or strongyles in the Palau specimen. This divergence of spicule characters is the only difference between the two specimens. Clearly, additional specimens from other localities are required before it can be definitely stated that the two are the same.

**DISTRIBUTION:** Ponapé, Caroline Islands (de Laubenfels).

#### FAMILY DESMOXYIDAE Hallmann

#### GENUS *Higginsia* Higgin

#### *Higginsia mixta* (Hentschel)

#### Fig. 26

*Dendropsis mixta* Hentschel, 1912, p. 415.

*Higginsia mixta* Hallmann, 1917, p. 656.

**OCCURRENCE:** Sta. 258.

**DESCRIPTION:** A thickly encrusting sponge with irregular digitiform processes arising over the whole surface.

**DIMENSIONS:** 3.8 cm high, 2.5 cm long, 0.6 cm thick.

**COLOR:** In alcohol, gray.

**TEXTURE:** Compact, compressible, and resilient.

**SURFACE:** Unevenly conulose, smooth between conules, hispid over-all but particularly at the apices of the conules and toward the ends of the erect processes.

**SKELETON:** Somewhat lax and irregular, with a tendency for concentration of ascending tracts toward the center of the vertical processes. Small patches of spongin occur along all spicule tracts, but no actual spongin-encased fibres occur. The long styles and stout oxeas form the ascending tracts and these curve out at an acute angle to the surface. In the subdermal region fine, centrally-angulate oxeas are added to the spicule tracts and these, with the huge styles,

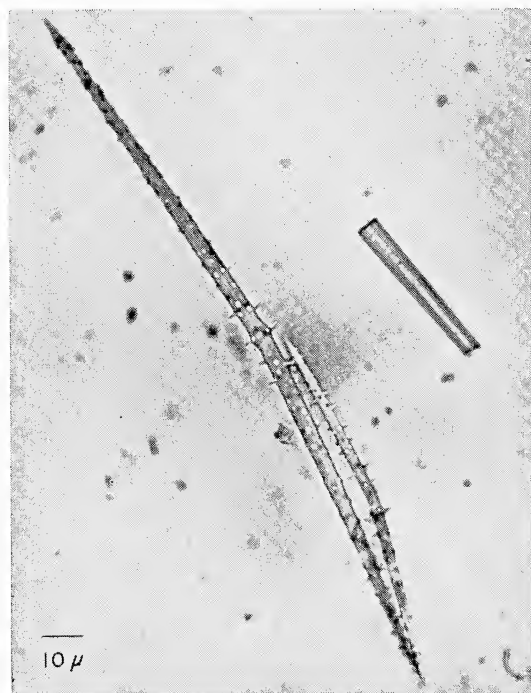


FIG. 26. *Higginsia mixta* (Hentschel). Sta. 258. Acanthoxeas.



are the spicules that project beyond the surface. Small centrally flexed acanthoxeas occur throughout the sponge, but are particularly abundant in the dermal membrane where they are oriented tangentially and form a marked crust.

**SPICULES:** *Megascleres*. (a) Long curved styles,  $1900-3125 \times 14.5-17.5\mu$  ( $2425 \times 16.4\mu$ ). These spicules occur at the center of all spicule tracts and usually extend outward through a surface conule surrounded by fine oxeads. (b) Stout oxeads,  $1025-1150 \times 16-20.8\mu$ , forming the bulk of the spicule tracts. (c) Slender, centrally-angulate oxeads generally disposed in subdermal tufts and piercing the surface around a large central style;  $650-912 \times 5.5-6.8\mu$  ( $792 \times 6.2\mu$ ).

*Microscleres*. Abundant acanthoxeas, finely spined, centrally-angulate often with a central belt of slightly larger spines. Frequent smooth spicules of similar dimensions occur; these are always centrotylote;  $62.5-200 \times 2-4.5\mu$  ( $132 \times 3.6\mu$ ).

**DISCUSSION:** This specimen compares in detail with *Dendropsis mixta* Hentschel. Hallmann (1917) has put forward a convincing argument for merging *Dendropsis* and *Higginsia*. Higgin and his nomenclature is adopted here. Burton (1959:256) has published a key to the species of *Higginsia* in which *H. mixta* is listed as having "main megascleres seldom exceeding 0.9 mm in length." Both Hentschel's specimen and the Palau specimen have two categories of megascleres, including the principal oxeads, which regularly exceed  $1000\mu$  in length.

**DISTRIBUTION:** Aru Islands (Hentschel).

#### GENUS *Myrmekioderma* Ehlers

*Myrmekioderma granulata* (Esper)

Fig. 27a, b

*Alcyonium granulatum* Esper, 1830, p. 71, pl. XXIV.

*Myrmekioderma granulatum* Ehlers, 1870, p. 28.

*Acanthoxifer ceylonensis* Dendy, 1905, p. 157, pl. IX, fig. 5.

*Acanthoxifer ceylonensis* Dendy, 1922, p. 129.

*Myrmekioderma granulatum* Burton, 1937, p. 39, pl. VII, fig. 42.

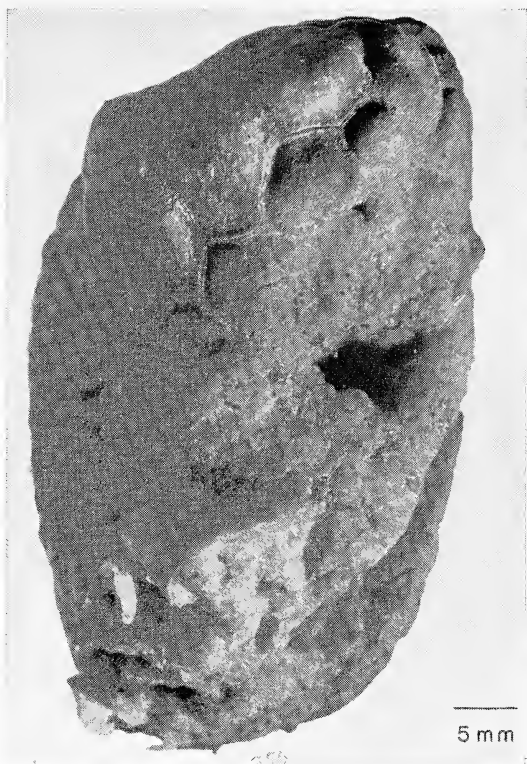


FIG. 27a. *Myrmekioderma granulata* (Esper). Sta. 594, Ifaluk.

*Myrmekioderma tylota* de Laubenfels, 1954, p. 119, fig. 74.

*Myrmekioderma granulata* de Laubenfels, 1954, p. 121, fig. 75.

*Neoprosypa atina* de Laubenfels, 1954, p. 190, fig. 127.

*Acanthoxifer fourmanoiri* Lévi, 1956, p. 5.

*Myrmekioderma granulata* Lévi, 1961, p. 14, fig. 17.

**OCCURRENCE:** Sta. 100, 220A, 59 Palau; 142, 155-157; 594 Ifaluk.<sup>11</sup>

**DESCRIPTION:** This sponge is massive to encrusting, occurring usually as a thin crust over coral or growing inside bivalve shells. The only

<sup>11</sup> Station data for Ifaluk localities: 142. Oct. 20, 1953. Lagoonward reef margin. West reef between Elargalap and NW end of Falarik Island. Depth 1 fathom. 155-157. Oct. 23, 1953. Lagoonward reef margin. SW reef. Transect E. between Elangalap islet and Ella islet. Depth 1 fathom. 594. Oct. 7, 1953. Ifaluk lagoon near the pass.

TABLE 11

SPECIMEN	LOCALITY	ENDOSOMAL MEGASCLERES	ACANTHOXEAS	MICROSCLERES	SURFACE
<i>Myrmekioderma granulata</i> Ehlers	East Indies	oxeas to styles 740-940 $\mu$	350-400 $\mu$	not mentioned	coarsely tuberculate
<i>Acanthoxifer ceylonensis</i> BM 1905	Gulf of Manaar	oxeas, strongyles, styles 700-(828)-1032 $\times$ 10.5-(12)-13 $\mu$	237-(337)-400 6.5-(9.5)-13 oxeas predominate, styles frequent, strongyles rare	trichodragmata (160 $\times$ 4 $\mu$ ), raphides up to 82 $\mu$ in length	tuberculate polygonal
<i>Myrmekioderma granulata</i> Ehlers Burton 1937	Gulf of Manaar	oxeas to styles ? 170 $\times$ 12 $\mu$	400 $\times$ 8 $\mu$	trichodragmata 16 $\times$ 4 $\mu$	tuberculate polygonal
<i>Myrmekioderma styx</i> de Laubenfels, 1953. USNM 23400	Gulf of Mexico 12.5 m	oxeas, styles, strongyles 650-(738) 800 $\times$ 11-(13.5)- 16 $\mu$	oxeas only 300-(337)-375 $\times$ 7- (19)-12.5 $\mu$	raphides or trichodragmata 20-50 $\mu$	coarsely tuberculate, with sunken "pore areas," finely hispid
<i>Myrmekioderma tylota</i> de Laubenfels, 1954. USNM 22059	Ponapé	oxeas, strongyles, styles 400-(625)-762 $\times$ 7- (10.5)-13 $\mu$	predominantly oxeas, strongyles and styles frequent 225-(372)-475 $\times$ 5- (8)-10 $\mu$	raphides up to 120 $\mu$ , trichodragmata 40-56 $\times$ 8-12 $\mu$	tuberculate with prominent grooves, smooth in places, finely hispid
<i>Myrmekioderma granulata</i> de Laubenfels, 1954. USNM 23073	Truk	oxeas, styles, strongyles 350-(542)-637 $\times$ 6- (9.3)-10.5 $\mu$	predominantly oxeas, strongyles and styles frequent 300-(332)-370 $\times$ 5- (7.5)-12 $\mu$	raphides up to 90 $\mu$ , trichodragmata 33-85 $\times$ 6-12 $\mu$	tuberculate, grooves plainly visible, occasionally smooth, finely hispid
<i>Neoprotypa atina</i> de Laubenfels, 1954. USNM 22974	Ebon Atoll	oxeas and strongyles 600-(666)-762 $\times$ 6- (7.2)-8 $\mu$	predominantly oxeas, styles frequent, strongyles rare 212-(334)-350 $\times$ 5- (6)-7.5 $\mu$	trichodragmata 33-65 $\times$ 6-10 $\mu$ , individual raphides up to 86 $\mu$	tuberculate, but smooth in places, very irregular owing to the incorporation of coral fragments; pores visible in surface grooves

TABLE 11 (Continued)

SPECIMEN	LOCALITY	ENDOSOMAL MEGASCLERES	ACANTHOXEAES	MICROSCLERES	SURFACE
Sta. 220 Palau	Iwayama Bay	oxeas, styles, strongyles 725-(863)-1062 $\mu$	312-(333)-362 $\times$ 6.5- (8)-10 $\mu$ oxeas, styles, and strongyles	trichodragmata 40-86 $\times$ 6-10 $\mu$ , individual raphides up to 120 $\mu$	tuberculate, much of the surface pattern obscured by fine debris; pores not visible; hispid
Sta. 594 Ifaluk		oxeas almost always mucronate, strongyles abundant, styles frequent 525-(647)-825 $\times$ 6.5-(8.3)-10.5 $\mu$	oxeas, styles, and strongyles 312-(332)-362 $\times$ 5.5-(6.5)-10 $\mu$	trichodragmata present in sections, individual raphides up to 115 $\mu$	tuberculate, pore grooves plainly visible, surface largely clear of debris, finely hispid
Sta. 100 Palau	Iwayama Bay	oxeas, strongyles also abundant, some styles 650-(788)-875 $\times$ 7- (12)-16.5 $\mu$	oxeas predominate, some styles and strongyles 287-(327)-375 $\times$ 6.5- (8.5)-11.5 $\mu$	raphides only in spicule preparations (no section pre- pared) up to 130 $\mu$	surface badly damaged
<i>Acanthoxifer fourmanouiri</i> Lévi, 1956	Madagascar Nossi bé	oxeas 600-800 $\times$ 10-12 $\mu$ , strongyles and styles 500-600 $\times$ 10-12 $\mu$	330-400 $\times$ 13-17 $\mu$	raphides in trichodragmata up to 160 $\mu$ long	hispid; covered with fine sand
<i>Myrmekioderma granulata</i> Lévi, 1961	Aldabra 42 meters	styles and oxeas 700-800 $\mu$	350-425 $\mu$	raphides up to 90 $\mu$	"hispid, excavated by deep irregular cavities"

In all cases the measurements quoted are based upon re-examination of type material; in the case of *Acanthoxifer ceylonensis* only a spicule mount was available.  
In all specimens examined trichodragmata are rare and measurements are based upon few examples.



FIG. 27b. *Myrmekioderma granulata* (Esper). (*Myrmekioderma tylota* de Laubenfels. Holotype.)

massive specimen is Ifaluk 594, the dimensions of which are 4.8 cm high, 6 cm wide, 3 cm thick.

**COLOR:** In alcohol, usually pale cream to pale yellowish (rY 8/4) overall, occasionally with a pink coloration (pR 5/4) in places.

**TEXTURE:** Firm, compact; somewhat fleshy and crumbly in the endosome.

**SURFACE:** In massive and thickly encrusting specimens the characteristic pattern of polygonal tubercles is clearly developed, although not necessarily over the whole surface; thinly encrusting specimens do not show this clearly. In all cases the surface is finely hispid. None of the present specimens is sufficiently well preserved to demonstrate the presence of pores in the grooves between the tubercles; these, however, show plainly in USNM 22974, the type of *Neoprosopa atina* de Laubenfels.

**SKELETON:** By far the most precise description of the skeleton of this species is given by Dendy (1905) for *Acanthoxifer ceylonensis*,

and this applies in detail to the Palau and Ifaluk specimens. The dense cortical or ectosomal region is composed of closely adjacent brushes of vertically disposed acanthoxeas. Toward the margins of the surface tubercles the orientation of the spicules changes from vertical to oblique. The spicule brushes thin out leaving gaps in the ectosomal skeleton corresponding with pore cracks; these open below into subdermal cavities which extend up to  $800\mu$  below the surface. Cortical acanthoxeas project up to  $180\mu$  beyond the sponge surface, rendering it hispid, maximally so over the central region of the tubercles.

The endosomal skeleton is basically a confused mass of acanthoxeas and larger, smooth, predominantly diactinal megascleres. At irregular intervals the large megascleres are organized into tracts originating at the base of the sponge and curving outward to the base of the ectosome. Small amounts of spongin are associated with these tracts.

**SPICULES:** *Megascleres.* (a) centrally-flexed to straight acanthoxeas with exceedingly fine, regular spines over the entire spicule, sometimes more abundant at the ends. Both stylote and strongylote modifications are frequent; the oxneas could often be better described as mucronate strongyles. These spicules are remarkably uniform in their range of size and shape in all of the specimens examined. Very slender developmental stages are frequent. (b) Long, relatively thin, smooth oxneas, strongyles, or, less frequently, styles, which make up the bulk of the endosomal skeleton. These spicules are frequently wavy; only in three specimens are straight and somewhat stouter spicules the rule (*Acanthoxifer ceylonensis*; USNM 22059; and Sta. 100). Many spicules of this category have either slightly stairstepped or mucronate tips.

*Microscleres.* Raphides in loose trichodragmata which, in all specimens examined, break up when the spicules are boiled in acid. Some single raphides occur. The length of these spicules is more variable than earlier reports indicated (Table 11).

**HISTOLOGY:** The ectosome is collenchymatous with a slight concentration of spongin A at the inner boundary. The endosome is cavernous, relatively fleshy, containing abundant

spherical flagellate chambers, 23–30 $\mu$  in diameter.

DISCUSSION: Dendy (1922) suggested the possible synonymy of his genus *Acanthoxifer* with *Myrmekioderma* Ehlers, the only difference between the two being the presence of trichodragmata in *Acanthoxifer*. Burton (1937) and Lévi (1961) have adopted this synonymy. De Laubenfels (1936), however, retained *Acanthoxifer* as a genus of the Rhaphidistinae but based his decision on a misinterpretation, having regarded the acanthose megascleres as a second category of microscleres which he termed "spiny microhabds." De Laubenfels (1954) recorded *Myrmekioderma granulata* (Esper) from Truk and described a new species, *Myrmekioderma tylota*, from Ponape, the latter differing from *M. granulata* in having small "tylotes" as microscleres instead of trichodragmata. In the same work a new genus of Hymeniacidonidae, *Neoprosypa*, was erected for the single species, *Neoprosypa atina*.

Comparison of the type specimens of *Myrmekioderma tylota* and *Neoprosypa atina* with de Laubenfels' specimens of *Myrmekioderma granulata* (see table) reveals that all these sponges are identical. The "small tylotes" of *M. tylota* are diatoms; further, trichodragmata do occur in this species.

A spicule preparation of the holotype of *Acanthoxifer ceylonensis* Dendy shows a very similar range in variation of spicule size and shape to that found in de Laubenfels' and in my Pacific specimens. Further, the surface features and skeletal arrangement correspond in detail.

Lévi (1956) described *Acanthoxifer fourmanoiri* from Madagascar and considered this distinct from *Acanthoxifer ceylonensis* Dendy in having longer raphides making up the trichodragmata and a tangential or oblique arrangement of dermal acanthoxeas. Dendy mentioned that many of the dermal spicules were obliquely disposed in *A. ceylonensis*. This disposition is characteristic of the sides of the surface tubercles in all of de Laubenfels' specimens and those from Ifaluk and the Palaus. With the description of a specimen of *Myrmekioderma granulata* from Aldabra, Lévi (1961) provided data which reduced the gap between the raphide

dimensions of *A. fourmanoiri* and other specimens of *M. granulata* from Ceylon and the central Pacific. The Palau specimens possess long raphides, as do de Laubenfels' specimens. The differences are not what they appear to be from the literature and do not justify the division of this genus into separate species.

In the generic diagnosis of *Neoprosypa* de Laubenfels states that "all or nearly all of the megascleres are completely acanthose." This is an error; the type specimen of *N. atina* has the minutely acanthose megascleres and also the smooth endosomal megascleres characteristic of *M. granulata*. The ectosomal megascleres are clearly set off from the endosome in *Neoprosypa atina*, but they tend to be oblique over large areas due to the extremely irregular habit of the sponge. In this respect *N. atina* approaches *A. fourmanoiri*. Lévi, Ehlers' (1870) redescription of *Alcyonium granulatum* Esper makes no mention of trichodragmata; these, however, are rare and inconspicuous in every Pacific specimen examined and, as de Laubenfels (1954) has pointed out, they could easily have been overlooked.

The position of *Myrmekioderma styx* de Laubenfels from the Gulf of Mexico is problematic. The holotype has been re-examined and few differences can be found to separate this species from the Indo-Pacific *M. granulata*. The surface is more coarsely and irregularly tuberculate and the skeleton is a vague and irregular endosomal reticulum of acanthoxeas broken by dense tracts of large oxeas and acanthoxeas, running vertically toward the ectosome. In the ectosome the acanthoxeas are either vertical in brushes, vertical but densely packed, or tangential to oblique. It is impossible to separate this specimen from others assigned to *M. granulata* on the basis of spiculation, and skeletal and surface differences are not conclusive. In view of the geographic discontinuity between *M. styx* and other specimens assigned to *M. granulata* the two species are retained at present.

The systematic position of *Myrmekioderma* Ehlers has been frequently debated. Dendy (1905) created the subfamily Heteroxyinae within the Haploscleridae to receive *Heteroxya* Topsent and *Acanthoxifer* Dendy (= *Myrmekioderma*). In 1922 Dendy suggested the

synonymy of *Acanthoxifer* and *Myrmekioderma* and removed the Heteroxyinae to the Desmacidonidae (Subfamily Axinellinae, section Heteroxyeae). Topsent (1928) elevated the Heteroxyinae to family rank, added *Anacanthaea* Row, and endorsed the relationship of the group to the Axinellidae. Burton (1937) placed *Myrmekioderma* in his section Raspeliaceae, which includes all axinellid families.

Wilson (1925) was unaware of the synonymy of *Acanthoxifer* with *Myrmekioderma* and referred *Acanthoxifer* and *Anacanthaea* to *Spongosorites* Topsent on the basis of Dendy's (1905) redefinition of this genus and information derived from study of a new sponge, *Spongosorites suluensis* Wilson. Wilson urged the relationship of the above sponges to the Epipolasida, as Jaspidae without microscleres. De Laubenfels (1936) has in part sustained this view in making *S. suluensis* Wilson the type of *Epipolasis*, which is placed in the Sollasellidae. This cannot, however, apply to *Acanthoxifer* and *Anacanthaea*; these sponges have their closest relatives in the genus *Higginsia*, to which they are closely allied in Dendy's 1922 classification. Wilson's reason for uniting the genera is that *S. suluensis* has tangential dermal oxeas on the oscular face (see *Spongosorites sensu* Dendy) and oxeas in radial brushes on its pore face; these characters are compared to *Acanthoxifer* and *Anacanthaea*. This is a simplification which entirely overlooks previous synonymy and certain structural features, such as the presence of a vague fibrous structure in the choanosome of *Acanthoxifer* (*Myrmekioderma*) accompanied by traces of spongin, and the variable disposition of the dermal oxeas in this genus. *Anacanthaea* does not possess a separate category of dermal oxeas. Furthermore, both genera share the distinctive surface pattern of polygonal tubercles delimited by pore grooves (Fig. 27a, b). None of these features has been recorded for *Spongosorites*.

Wilson was correct in his assessment of the systematic position of *S. suluensis*;<sup>12</sup> he was in error in assuming *Spongosorites* to be a homogeneous genus. A proper evaluation of the re-

lationships of *Spongosorites* Topsent and *Epipolasis* de Laubenfels is urgently required but must await the restudy of type material.

De Laubenfels (1936) placed *Acanthoxifer* in the Epipolasida (Rhaphidistinae), *Heteroxya* in the Coelosphaeridae, *Anacanthaea* in the Axinellidae, and *Myrmekioderma* in the Phorbasidae, thereby rejecting the opinions of all previous authors. In the case of *Heteroxya* and *Myrmekioderma* he expressed doubts as to their correct placing; in the case of *Acanthoxifer* he misread the type description; *Anacanthaea* was placed with the axinellids on the tenuous ground that the spicules are stairstepped and mucronate.

It is not at all clear that *Heteroxya* Topsent is as close to *Myrmekioderma* and *Anacanthaea* as Dendy considered. *Heteroxya* has in common with the other two genera a densely spiculiferous cortex composed of radially disposed acanthoxeas, a hispid surface, and the large, smooth oxeas. It differs in morphology of the surface, in the scarcity of endosomal megascleres, lack of raphides, and in spicule size and shape. There is no mention of variability in spicule terminations in *Heteroxya* as reported for *Myrmekioderma*. The endosomal megascleres in *Heteroxya* are extremely large ( $2000 \times 35\mu$ ) and project beyond the surface; the acanthoxeas are  $235 \times 12-23\mu$ , much stouter than in *Myrmekioderma*. None of the above features, however, supports a coelosphaerid affinity for *Heteroxya* as de Laubenfels suggested.

At present the morphological evidence supports Dendy's decision that *Myrmekioderma* and *Anacanthaea*, with the possible addition of *Heteroxya*, should be placed near *Higginsia*, in a family close to the Axinellidae.

DISTRIBUTION: East Indies (Esper); Gulf of Manaar (Dendy 1905, Burton 1937); Coetivy (Dendy 1922); Truk, Ponape, Ebon (de Laubenfels); Madagascar, Aldabra (Lévi).

#### ORDER HADROMERIDA Topsent

#### FAMILY SPIRASTRELLIDAE Hentschel

#### GENUS *Spirastrella* Schmidt

*Spirastrella aurivilli* Lindgren  
Fig. 28a, b

<sup>12</sup> The type specimen of this sponge, USNM 21297, has been re-examined.

*Spirastrella aurivilli* Lindgren, 1897, p. 484.

*Spirastrella aurivilli* Lindgren, 1898, p. 322, pl. 17, fig. 11, pl. 18, fig. 4.

*Spirastrella aurivilli* Vosmaer, 1911, p. 21, pl. 19, fig. 22a-c.

*Spirastrella aurivilli* Burton, 1934, p. 571.

*Cliona aurivilli* de Laubenfels, 1936, p. 154.

OCCURRENCE: Sta. 92A, 258.

DESCRIPTION: The specimen from Sta. 92 is damaged, the other is entire and in good condition. It fills a cavity,  $9.5 \times 7.5 \times 16$  cm, inside coral limestone; 0.5–1.5 cm of coral remains surrounding the central sponge mass. The sponge produces numerous hollow papillae with slightly expanded flattened tips. These run to the surface through straight channels obviously bored by the sponge. They range from 0.8–12 mm in internal diameter, up to 18 mm in external diameter, and extend up to 3.5 cm above the surface of the rock. A great number of papillae are flush with the surface of the rock or project only 1–2 mm from the channels; these always have a single opening. Many

of the larger papillae are irregular and bear 2–3, rarely 6 openings, each terminal upon a stout branch of the axial papilla.

COLOR: In alcohol, dull pinkish-red (R 5/2).

TEXTURE: The central mass is soft and rubbery; the papillae are hard, stiff, and relatively brittle.

SURFACE: The external surface of the papillae is finely hispid and lumpy, reminiscent of many massive species of *Spirastrella*. The terminal region of the papillae is usually markedly irregular, suggesting that contortion is a temporary condition resulting from contraction of all external openings.

SKELETON: Lindgren's (1898) description of the disposition of the skeleton in *S. aurivilli* forma *excavans* applies with slight alteration to this specimen. In Lindgren's specimen the spirasters were not only absent from the papillae but were rare in the interior of the sponge; the large tylostyles were also rare.

In the specimen from Sta. 92 the spirasters are extremely abundant in the base; large tylostyles are abundant throughout both speci-

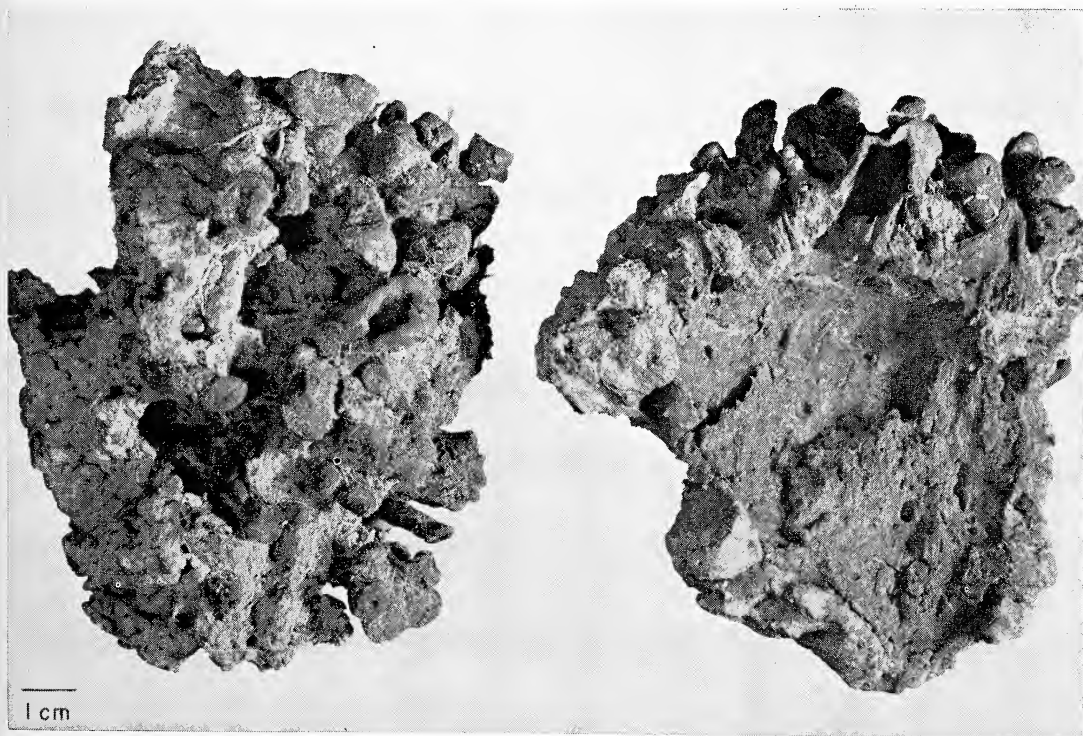


FIG. 28a. *Spirastrella aurivilli* Lindgren. Sta. 258.



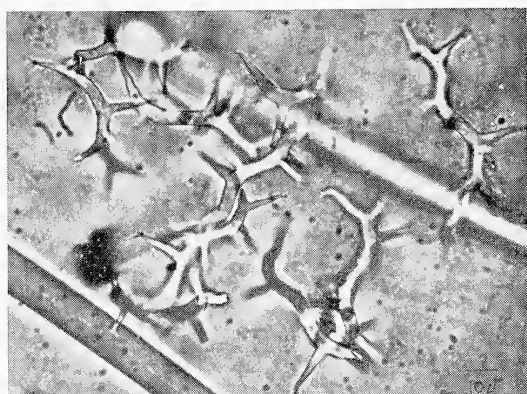


FIG. 28b. *Spirastrella aurivilli* Lindgren. Spirasters.

mens. The tylostyles constitute almost the entire skeleton of the papillae and are arranged in two distinct layers, an inner vertical layer and a central layer. A few tylostyles possibly constitute a third, dermal layer at right angles to the surface.

**SPICULES:** *Megascleres*. Tylostyles, of two size groups: (a) large, stout, straight or slightly curved tylostyles in which the head is most often subterminal. These spicules make up the bulk of the skeleton;  $500\text{--}680 \times 18\text{--}33\mu$ . (b) Smaller tylostyles with a great range in length and diameter and always with subterminal heads. The finer spicules tend to be found in the dermal spicule brushes of the sponge base;  $250\text{--}525 \times 7\text{--}16.5\mu$  ( $356 \times 10.5\mu$ ).

*Microscleres*. Large spirasters with stout, somewhat contort axes, at irregular intervals producing long branches which frequently have bifurcate tips;  $36\text{--}50\mu$  ( $42\mu$ ), shaft;  $3.0\text{--}5.0\mu$  thick.

**DISCUSSION:** *Spirastrella aurivilli* was referred to *Cliona* by de Laubenfels (1936:154) on the basis of Burton's remarks on the three species of *Spirastrella* found on the Great Barrier Reef. Burton (1934) clearly stated that young stages of *Spirastrella inconstans* Dendy and specimens of *Spirastrella aurivilli* are capable of boring. At the same time he noted that the excavations were always of simple type and showed little resemblance to the complex galleries of *Cliona*.

In neither of the Palau specimens is there any trace of complex boring; the inhalant and exhalant tubes lead through simple straight channels in the coral.

The distinctive microscleres and predominantly boring habit of *S. aurivilli* serve to differentiate the sponge from the vast complex which Vosmaer (1911) includes in *S. purpurea*.

**DISTRIBUTION:** Java Sea (Lindgren); Great Barrier Reef (Burton).

### *Spirastrella vagabunda* Ridley

#### RESTRICTED SYNONYMY:

*Spirastrella vagabunda* Ridley, 1884, p. 468.

*Spirastrella vagabunda* var. *trincomaliensis* Ridley, 1884.

*Spirastrella vagabunda* Dendy, 1905, p. 122.

*Spirastrella vagabunda* Wilson, 1925, p. 343.

*Anthosigmella vagabunda* de Laubenfels, 1954, p. 201, fig. 136, pl. ix, fig. b.

**OCCURRENCE:** Sta. 12, 92, 124.

**DESCRIPTION:** Specimens from Sta. 12 and 92 are massive, digitate, with prominent oscules on the flattened tips of the branches and can be compared closely with de Laubenfels' specimens (1954: pl. ix, b). The third specimen (Sta. 124) is a small subspherical sponge with a nodulose surface and prominent oscules scattered on the upper surface. It is probable that this represents only the apical portion of a branch of a sponge similar to the above. *S. vagabunda* usually lies buried in the sand and the terminal portions of branches appear capable of constricting and detaching from the parent body, possibly serving as a means of asexual reproduction.

Only a few facts about these specimens will be given to indicate how they differ from previously described specimens.

Two specimens (Sta. 12 and 92) conform closely in morphology to *S. vagabunda* as understood by most authors, having the dermal layer of outwardly directed small tylostyles, a dermal crust of spirasters, and lacking a second larger microscle category.

The megasccleres of the third specimen (Sta. 124) range from styles, to tylostyles (with terminal subterminal and polytylote heads), to tylostrongyles, and tend to be finer than the tylostyles of the other specimens. The cortex is without special organization, constituted of closely packed, interlacing spicules, the smaller types, styles and tylostyles, predominating. The

TABLE 12

SPECIMEN	TYLOSTYLES	SPIRASTERS
Sta. 12	300–687 (515) $\times$ 6–20 (13)	13.5–17 (15.5)
Sta. 92	290–635 (408) $\times$ 6.5–23.5 (14.5)	9–15 (16)
Sta. 124	250–637 (440) $\times$ 5.5–15 (9.9)	13–24 (18)

variability of the spicules in this sponge has already been noted by Dendy (1905) for *S. vagabunda* var. *trincomaliensis*. The cortical structure is comparable to that described for the type of *S. vagabunda* Ridley (1884). Microscleres in this specimen are extremely rare.

SPICULE DIMENSIONS (in  $\mu$ ) (Table 12).

DISCUSSION: De Laubenfels (1951, 1954) advocates retaining *Spirastrella* for four species, *cunctatrix*, *decumbens*, *coccinea*, and *potamophora*. All of these are considered to be persistently encrusting; the massive species are removed to other genera, in the case of *S. vagabunda* to *Anthosigmella*. *Anthosigmella* Topsent is defined essentially on the possession of anthosigmas, peculiar microscleres with short, truncate spines aligned on the convex surface of a C- or S-shaped spiraster. Certainly, some authors have described spirasters with spines restricted to the convex surface for *S. vagabunda* (e.g., Dendy, 1905); these were, however, present as an extreme variant of the normal spiraster. Nothing comparable to the anthosigma of *Anthosigmella varians* (Duchassaing and Michelotti), the type species of *Anthosigmella*, has ever been described for *S. vagabunda*. De Laubenfels himself (1954) comments on the rarity of such microscleres and on their irregularity in his Pacific specimens.

Vosmaer (1911), while creating extensive synonymies within *Spirastrella* which have been subsequently rejected by most authors, did produce a great deal of evidence for the fact that no species of *Spirastrella* described up to that time was persistently encrusting. De Laubenfels' decision to restrict *Spirastrella* was arbitrary; he produced no facts to support his con-

tention and made no attempt to reassign species other than *S. vagabunda*, which he assigned incorrectly.

DISTRIBUTION: Torres Straits (Ridley); Trincomalle, Ceylon (Carter); Mergui archipelago (Carter); Indian Ocean (Dendy, 1921); Philippines (Wilson, 1925); central Pacific (de Laubenfels, 1954).

#### GENUS *Timea* Gray

##### *Timea granulata* n. sp.

Fig. 29

OCCURRENCE: Sta. 53 (Holotype, USNM 23699).

DESCRIPTION: A thinly encrusting sponge, up to 0.5 mm thick, covering an area of approximately 3.0 sq cm on a coral fragment around the base of *Tetilla microxea*.

COLOR: In alcohol, pale brown.

SURFACE: Unevenly hispid and finely granular owing to the concentration of microscleres in the dermal region. No apertures are visible and much coarse calcareous debris is distributed over the surface.

SKELETON: Basically a confused mass of tylostyles which in isolated patches are organized into vertically disposed brushes. The larger tylostyles are always vertical and often project up to 200 $\mu$  beyond the sponge surface. Both types of microscleres occur in a dense dermal crust.

SPICULES: *Megascleres*. Tylostyles, varying greatly in length and width with terminal and rounded or subterminal, ovate heads tapering evenly to sharp points; 170–687  $\times$  1.5–8 $\mu$  (401  $\times$  4 $\mu$ ).

*Microscleres*. Chiasters, of two distinct size groups but identical structure. Six to nine stout

rays diverging from a centrum, the diameter of which is equal to approximately half the length of the rays. Each ray is terminated by four to six short conical spines. Occasional spicules have one or two rays, or some of the terminal spines reduced to irregular protuberances. The two groups are: (a) larger, and extremely abundant,  $13\text{--}16.5\mu$  ( $14.8\mu$ ), and (b) smaller, common, but less than 3% of total,  $4.0\text{--}5.8\mu$  ( $4.8\mu$ ).

DISCUSSION: Separation of the species of

*Timea* rests to a great extent on the form and variety of the microscleres. In this respect *T. granulata* is closest to *Timea* (*Hymedesmia*) *trigonostellata* (Carter) from the Gulf of Manaar, differing from this specimen chiefly in the size and shape of the megascleres. Those microscleres in which the rays are reduced can be compared with the lophasters of *Timea* (*Hymedesmia*) *lophastraea* Hentschel. In this species, however, all the microscleres are lophasters, small amphioxeas occur as supplementary spicules, and most of the megascleres are styles.

In several species of *Timea* (e.g. *hallezi*, *mixta*, *bistellata*, *squamata*) there is great variability in the terminations of the microsclere rays. *T. granulata*, with *T. trigonostellata* and *T. lophastraea*, is remarkably constant in this respect.

#### FAMILY PLACOSPONGIIDAE Gray

#### GENUS *Placospongia* Gray

#### *Placospongia melobesioides* Gray

#### RESTRICTED SYNONYMY:

*Placospongia melobesioides* Gray, 1867, p. 127.

*Placospongia melobesioides* Vosmaer and Vernhout, 1902, p. 13, pl. 1, fig. 5-9, pl. 11, fig. 1-4, fig. 6, pl. 111, pl. IV, fig. 1-8, pl. V, fig. 2, 6, 10, 12.

*Placospongia melobesioides* de Laubenfels, 1954, p. 220, fig. 152.

#### OCCURRENCE: Sta. 220A.

REMARKS: The species is represented by several large pieces of a single ramose sponge. It compares in detail with specimens described by earlier authors (Vosmaer, de Laubenfels) from various Indo-Pacific localities. The presence of small irregular spheres (up to  $2.0\mu$  in diameter) among the microscleres is a diagnostic character of *P. melobesioides*.

DISTRIBUTION: Wide Indo-Pacific distribution.

#### ORDER EPIPOLASIDA Sollas

#### FAMILY JASPIDAE de Laubenfels

#### GENUS *Asteropus* Sollas

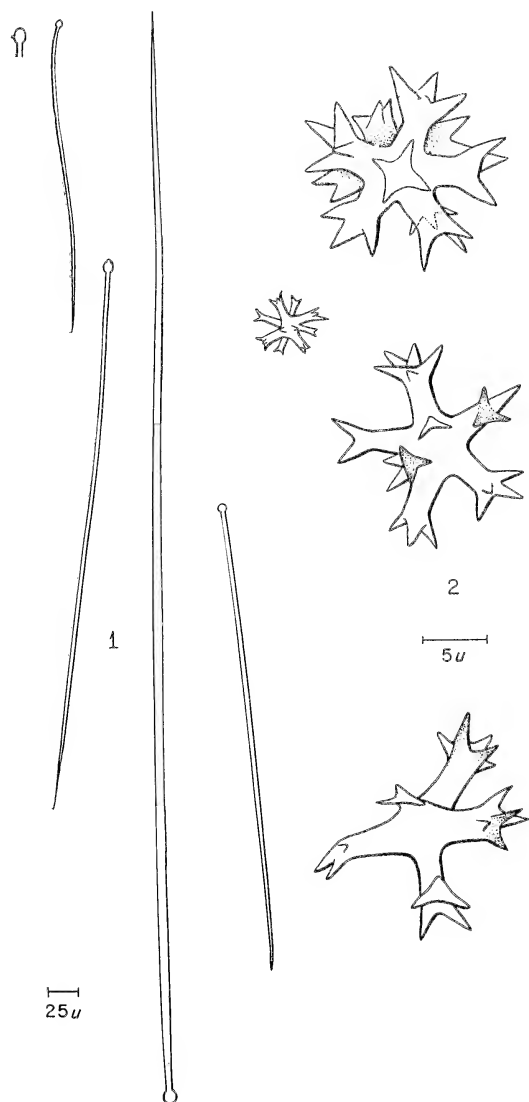


FIG. 29. *Timea granulata* n. sp. Sta. 53. Holotype. USNM 23699. Spicules: 1, Tylostyles. 2, Chiasters.



FIG. 30a. *Asteropus sarasinorum* (Thiele). Sta. 136.

*Asteropus sarasinorum* (Thiele)

Fig. 30a, b, c

*Melophus sarasinorum* Thiele, 1899, p. 8, pl. 1, fig. 2, pl. 5, fig. 3.

*Jaspis bandae* Brøndsted, 1934, p. 8, fig. 4, 5, 6.

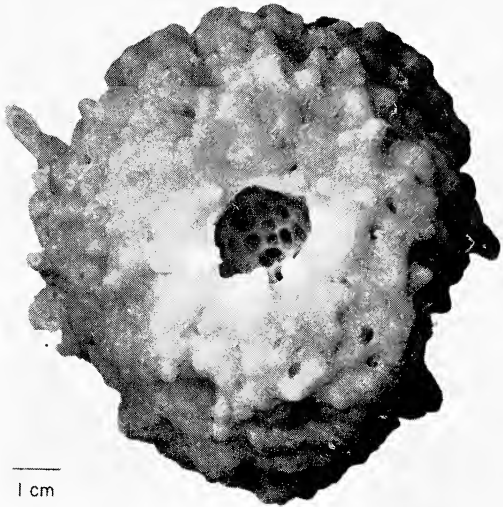


FIG. 30b. *Asteropus sarasinorum* (Thiele). Apical view showing the cloacal opening and the openings of the exhalant channels to the base of the cloaca.

*Stellettinopsis isis* de Laubenfels, 1954, p. 221, fig. 153, pl. 10, a.

OCCURRENCE: Sta. 136, 252.

DESCRIPTION (Table 13).

The intact specimen compares in detail with *Stellettinopsis isis*, which is well described and figured by de Laubenfels. The larger specimen which has been cut into thirds (one part of which is missing) is identical with the figures of *Melophus sarasinorum* Thiele and *Jaspis bandae* Brøndsted. The surface processes fring-

TABLE 13

SPECIMEN	SHAPE AND SIZE			CLOACA		THICKNESS FROM CLOACA TO EXTERIOR
	Height	Width	Depth	Diameter	Depth	
Sta. 136	18 cm	10.5 cm centre 6.5 cm apex	7.5 cm	1.8 cm	5 cm	
Sta. 252 (incomplete specimen)	22 cm	—	—	contracted	12 cm	5 cm base 2.5 cm apex

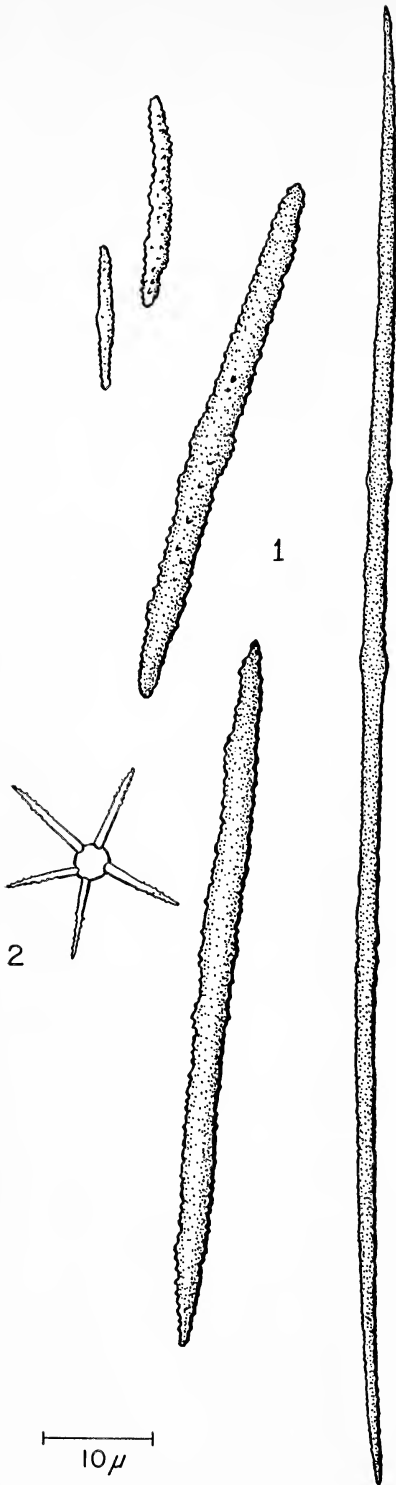


FIG. 30c. *Asteropus sarasinorum* (Thiele). Microscleres: 1, Microxeas of three size categories. 2, Euaster.

ing the cloacal opening are more pronounced in the younger specimens, the surface pattern of pores and tubercles is more regular and the ectosome is thinner.

*Jaspis bandae* was described from an entire, dried specimen and no mention is made of a cloaca. One of the Palau specimens has contracted upon fixation in such a way as to almost obscure the cloacal opening; it is possible that *Jaspis bandae* possesses a cloaca similarly hidden by contraction.

COLOR: In alcohol, straw color (rY 8/4).

TEXTURE: Variable. Stiff but compressible, somewhat waxy, in the smaller specimen, to hard, just compressible, almost woody, in the larger sponge.

ECTOSOME: This layer is often thicker than de Laubenfels (1954:223) states, varying from 2–4 mm. In all other details of ectosomal and endosomal structure and disposition of the skeleton, de Laubenfels' description cannot be added to.

SPICULES: *Megascleres*. (a) Oxeas, of extremely variable dimensions, not, however, as stout as the maximum diameter quoted by other authors (Table 14). The ends are often stair-stepped on the larger spicules, and most spicules are slightly bent in the middle. A great number of spicules are about  $800 \times 10\mu$ – $15\mu$ . (b) Styles, occasional only; they appear to be modifications of the smaller oxeas.

*Microscleres*. (a) Microxeas, varying from small, microspined, centrotylote rhabds extremely similar to those of *Ancorina*, to large, straight or slightly curved, finely spined and often centrotylote microxeas. It is possible to select three size groups of these spicules as Brøndsted (1934) has done. Intermediates regularly occur, however, and it is safe to regard these spicules as all of one type. The small rhabds are concentrated as a surface layer 12– $15\mu$  deep. They also occur scattered throughout the ectosome and abundantly throughout the endosome where they intermingle with the larger microxeas. (b) Asters, with microspined rays, usually pointed, but often strongylote or truncate. The tylote modification figured by Brøndsted for *Jaspis bandae* has never been observed.

DISCUSSION: This sponge can be considered

congeneric with Carter's *Stellettinopsis simplex* which Sollas (1888) has made the type of *Asteropus*. *Asteropus* has been used subsequently by Hentschel (1909) and Dendy (1905, 1916, 1924); until recently only de Laubenfels persisted in the use of *Stellettinopsis*. He has added three new species, *ketostea*, *isis*, and *kaena*. Lévi (1961) has described *S. cherbonnieri*.

Sollas mentioned (1888:201) that *Stellettinopsis corticata* Carter, which was designated as the type species of the genus *Stellettinopsis* by de Laubenfels (1936), possessed triaenes and was, consequently, generically distinct from *S.*

*simplex*, which lacked triaenes. Sollas then took the rather unwarranted action of dropping *Stellettinopsis* entirely and erecting a new genus, *Algol*, for *S. corticata*. De Laubenfels is correct in regarding *Algol* Sollas as a synonym of *Stellettinopsis* Carter which is doubtfully distinct from *Ancorina*; he is, however, incorrect in persisting in the use of the name *Stellettinopsis* for sponges which consistently lack triaenes.

*Stellettinopsis corticata* Carter must be placed among the Ancorinidae; its possible synonymy with *Ancorina* can be decided only after a re-examination of the type specimen.

All other species described in *Stellettinopsis*

TABLE 14

SPECIMEN	OXEAS	MICROXEAS	ASTERS
<i>Melophus sarasinorum</i> Thiele, 1899 Celebes	1330 × 50μ	175 × 4μ 60 × 6μ 18-20 × 3μ	15-18μ 15-20 rays often strongylote
<i>Jaspis bandae</i> Banda Neira East Indies	1000-1200μ 35-40μ Styles 800-900 × 35-40μ	120-150 × 4-5μ 25-28 × 3-4μ 9 × 3μ all intermediates occur	15-25μ 8-12 rays strongylaster to tylaster
<i>Stellettinopsis isis</i> de Laubenfels, 1954 Palau Is.	1230 × 44μ (maximum) 1000 × 20μ (common)	60 × 3μ 45 × 4μ 18 × 3μ	12μ 10-15 rays euasters
Sta. 136, Palau	730-1080 × 9.5-28μ (969 × 21μ) Styles 850-925 × 15-17μ	range of all groups 10-135 × 2-4.5μ individual categories { 120-135 × 3-4.5μ 28-50 × 2.5-3μ 12-20 × 2-3μ	12-19μ (14μ) euasters to strongylasters
Sta. 252, Palau	875-1150 × 6-33μ (964 × 18.5μ) Styles 880-987 × 15-20μ	range of all groups 9-150 × 2-5.5μ individual categories { 125-150 × 3-4μ 30-70 × 2-5.5μ 9-20 × 2-3.5μ	11.5-20μ (15μ) 8-20 (approx.) rays euasters to strongylasters
<i>Stellettinopsis isis</i> de Laubenfels, USNM 23137 TYPE	575-1150 × 11-39μ (943.5 × 25μ) strongyloxeote spicules occur throughout this range	range of all groups 9-150 × 2-4μ (the larger microxeas are rare in this specimen) 125-150 × 2.5-3.5μ other categories as quoted by de Laubenfels	11.5-18 (14.5μ) 10-20 rays (approx.) euasters to strongylasters

must be transferred to *Asteropus*.<sup>13</sup> The systematic position of this genus is difficult to ascertain. However, since the absence of triaenes in *A. simplex* (Carter) is well authenticated,<sup>14</sup> and no rare or malformed triaenes have been reported for other species, it seems permissible to leave *Asteropus* in the Epipolasida.

Within this genus as at present defined there are two groups of species based upon microscle content: (1) *Asteropus simplex*, *A. ketostea*, and *A. kaena* having streptasters which are often termed sanidasters or scepterelliform asters; (2) *Asteropus sarasinorum*, (Thiele) with diactinal microscleles varying from *Ancorina*-like rhabds to substantial micoxeas, and *Asteropus cherbonnieri* (Lévi), which lacks the smaller rhabds. Should a new generic name eventually be required for the latter group then *Melophus* Thiele should be used. An analagous situation is that of *Ancorina* Schmidt (with sanidasters) and *Ecionemia* Bowerbank (with miciorhabds); all recent authors consider these to be synonyms.

With regard to the synonymy of *Asteropus sarasinorum* (Thiele), there is no doubt after examination of the type of *S. isis* (USNM 23137) and the Palau specimens that these are conspecific with *Melophus sarasinorum* Thiele from the Celebes. De Laubenfels has three times misrepresented this species in the literature. In 1936 (p. 70) he referred *Melophus* to the Adociidae. In 1950 he corrected this and stated that *Melophus* lacked asters, giving this as the main reason for not uniting *Melophus* and *Stellettinopsis*. Thiele (1899) described and figured asters in *Melophus sarasinorum*, the only species in the genus. Finally, de Laubenfels (1954)

proposed the synonymy of the two genera but considered *sarasinorum* to be distinct from *isis*. In support of this contention he cited the small size of *sarasinorum*. Thiele, however, stated that his specimen was 20 cm high and 14 cm wide, a size quite comparable with that of *Stellettinopsis isis*.

*Jaspis bandae* Brøndsted is closely comparable with both *M. sarasinorum* and *S. isis*. The specimen was dried and consequently details of internal anatomy are not available.

DISTRIBUTION: Celebes (Thiele); East Indies (Brøndsted); Palau Islands, Truk Island (de Laubenfels).

#### GENUS *Jaspis* Gray

*Jaspis coriacea* (Carter)

*Stellettinopsis coriacea* Carter, 1886, p. 126.

*Coppatias coriaceus* Sollas, 1888, p. 207.

*Jaspis coriacea* de Laubenfels, 1936, p. 151.

OCCURRENCE: Sta. 106.

DESCRIPTION: An irregularly massive to encrusting sponge which binds large pieces of coral and shell debris. The over-all size of the sponge is 8.5 × 5.5 cm, up to 3.5 cm thick.

COLOR: In alcohol, pinkish-white externally, flesh color internally.

TEXTURE: Firm, compressible.

SURFACE: A great proportion of the surface is covered with adhering shell fragments; the clear regions are hispid and minutely granular.

SKELETON: A thin dermal region is marked by the presence of a dense crust of microscleles and some tangential oxeas. Below this is an ectosomal layer, a region of large subdermal cavities bounded internally by a dense zone of spongin A. Some spicule tracts traverse this region, others end internally to it; those that traverse the ectosome are accompanied by relatively large concentrations of spongin. Abundant large cells with granular cytoplasm occur toward the inner boundary of the ectosome. The endosomal skeleton is made up of tracts of oxeas disposed radially and diverging toward the surface. The irregular habit of the sponge inhibits the development of a radial skeleton in many regions and the tracts become tangential and somewhat confused. Two

<sup>13</sup> With the exception of *Stellettinopsis annulata* Schmidt, which Topsent (1923) has referred to *Sphinctrella*, and *S. carteri* Ridley, *S. coriacea* Carter, *S. lutea* Carter, *S. purpurea* Carter, and *S. tuberculata* Carter, all of which were referred to *Coppatias* by Sollas (1888) and which consequently fall into *Jaspis*. The last four species are all considered to be synonyms of *Jaspis stellifera* (= *Jaspis coriacea*) by Shaw (1927); this synonymy requires further evidence since the type descriptions of *S. coriacea* and *J. stellifera* are not at all comparable.

<sup>14</sup> Dendy (1924) has mentioned occasional malformed oxeas and triaene derivatives in *Asteropus simplex* from New Zealand.



types of oxeas occur. The larger make up the bulk of the skeleton; the finer, smaller spicules occur principally in the endosome, in and between the radial tracts and less abundantly in the cortex where they are scattered tangentially. There is no well-defined layer of cortical oxeas.

**SPICULES:** *Megascleres*. Oxeas of two size groups: (a) large, straight, evenly tapered to sharp points, occasionally stylote;  $737\text{--}1712 \times 11\text{--}30\mu$  ( $1272 \times 18.7\mu$ ), and (b) small, fine identical in form to the larger;  $200\text{--}587 \times 1.5\text{--}3.5\mu$  ( $356 \times 3.5\mu$ ).

*Microscleres*. Euasters, occasionally modified to strongylasters, with 8–15 rays and centrum with diameter approximately one third the length of the rays;  $5.2\text{--}12\mu$  ( $8\mu$ ).

**DISCUSSION:** Dendy (1916:252) gives an excellent synopsis of the early history of the generic nomenclature of *Jaspis* Gray and *Coppatias* Sollas, and his conclusions as to the synonymy of these genera have been supported by all later authors. *Stellettinopsis coriacea* Carter is the type species of *Coppatias* Sollas and is thus, presumably, entirely typical of *Jaspis* except that there is slightly greater organization of the skeleton into radial tracts. The Palau specimen indicates that this feature is extremely variable, being somewhat dependent upon the habit of the sponge.

*Jaspis coriacea* from the Palau Islands corresponds in detail with Carter's rather fragmentary type description, the only discrepancy being the slightly larger size of the smaller oxeas. Dendy (1916) has commented on the difficulty of deciding whether these spicules are microscleres or megascleres. In view of their shape, size, and disposition in the Palau specimen, it is likely that they are megascleres.

**DISTRIBUTION:** South Australia (Carter).

#### ORDER CHORISTIDA Sollas

#### FAMILY ANCORINIDAE Gray

#### SUBFAMILY ANCORININAE de Laubenfels

#### *Ancorina acervus* (Bowerbank)

Fig. 31a, b

#### RESTRICTED SYNONYMY:

*Ecionemia acervus* Bowerbank, 1862, p. 1101, pl. lxxiii, fig. 1.

*Ecionemia acervus* Bowerbank, 1873, p. 322, pl. xxx, figs. 1–6.

*Stelletta bacillifera* Carter, 1887, p. 78, pl. vi, figs. 9–14.

*Ecionemia bacillifera* Burton, 1937, p. 5, pl. 1, fig. 2.

*Hezekia walkeri* de Laubenfels, 1954, p. 236, fig. 163.

*Ecionemia spinastra* Lévi, 1958, p. 8, fig. 3.

*Ecionemia acervus* Burton, 1959, p. 194.

**OCCURRENCE:** Sta. 220A Palau (two large specimens); Ifaluk 32F; 41D; 42D (2 specimens); 49C; 50B; 65D; 87F; 88E; 197–198C; 208C; 344; 690 (2 specimens); 798.<sup>15</sup>

**DESCRIPTION:** An encrusting to massive sponge which in the present collections is growing upon coral fragments, bivalve shells, and *Halimeda*. The size range is considerable, from a small hemispherical sponge (Ifaluk 41-D5) to a massive specimen (220A-1) unfortunately incomplete, but at least 120 cm long and 5 cm thick.

**COLOR:** De Laubenfels (1954) gives field observations on the color of this sponge and the range that he quotes covers all color variants listed by Burton (1937). The Palau and Ifaluk specimens are grayish to fawn in alcohol, between (yYR 8/2) and (yYR 6/2). The surface is irregularly mottled with dark brown R-Y-R 3/2 in almost all specimens.

**SURFACE:** Appears generally smooth and

<sup>15</sup> Station data for Ifaluk localities:

32F. Sept. 4, 1953. Reef east of the south end of Falarik Island. Intertidal.

41D, 42D, 49C, 50B. Sept. 17, 1953. Reef east of the south end of Falarik Island. Covered by a few inches of water at low tide.

65D. Sept. 21, 1953. Western reef between Elangalap islet and the north end of Falarik Island. Intertidal.

87F, 88E. Sept. 29, 1953. Inner reef flat, 70 ft from shore; reef east of the south end of Falarik Island. Intertidal.

197–198C. Oct. 31, 1953. Reef east of the east end of the channel between Falarik and Falalap. Intertidal.

208C. Sept. 30, 1953. SW reef between Ella and Elangalap islets. 4–20 ft.

344. Sept. 20, 1953. Seaward shore of Elangalap. Lowtide.

690. Oct. 22, 1953. Seaward reef at south end of Falarik.

798. Oct. 31, 1953. South end of Falarik, seaward reef.



FIG. 31a. *Ancorina acervus* (Bowerbank). Sta. 220A.

granular; in places it is coarsely hispid and is microhispid over-all. Oscules are small, concentrated in dorsal or lateral oscular areas which measure up to  $1.8 \times 1.0$  cm. Individual oscules are circular or oval, ranging from 0.4–2.0 mm in maximum dimensions. In specimen 798 from Ifaluk, skeletal pores approximately 0.1 mm in diameter are visible over most of the surface.

**SKELETON:** The endosomal skeleton is made up of radially disposed oxeas which vary greatly in size and abundance; near the surface oxeas give way to small orthotriaenes with rare protriaenes, anatriaenes, and large orthotriaenes in that order. Between the cladomes of the surface orthotriaenes is a layer of radially disposed small oxeas. The most abundant microscleres are microspined microrhabds and these are aggregated at the surface to form a dense crust. The sponge is weakly corticate. The cortex is the region containing the clads of the triaenes and the radial oxeas, a densely spiculiferous zone containing some collenchymatous tissue; it is clearly separate from the endosome in the deeper region of which fleshy tissues predominate over skeletal elements.

Apart from the microrhabds which occur abundantly throughout the sponge, the distribution, relative abundance, and form of microscleres is extremely variable.

In the holotype of *Hezekia walkeri* (USNM 22925) and the two specimens from the Palau, anthasters occur in tracts deep in the endosome; these spicules are very sporadically distributed and only fortuitously seen in sections. Fine tylasters also occur, chiefly in the endosome lining large canals, but they are occasionally present in superficial spicule preparations. In all of the Ifaluk specimens anthasters are lacking, and tylasters with long, fine rays and small tylospherasters are the endosomal microscleres. In addition the microrhabds of these specimens are thinner and more finely spined than those of the Palau group. The specimens having anthasters can be compared with *Stelletta truncata* Kieschick (1898), those with tylospherasters approach very closely to *Ecionemia acervus* Bowerbank. Burton (1937) has produced evidence for the view that these two types are extremes in a single variable species.

**SPICULES:** *Megascleres* (Table 15). These spicules are essentially the same as described by all earlier authors, the only variability being in the presence or absence of protriaenes (present but rare in all specimens from the Palau) and in the length of the cladi of the anatriaenes, which are somewhat longer in the Palau specimens than in the Ifaluk group.

**Microscleres.** Three types are present in each sponge: (a) spined microrhabds, which are uniformly abundant, varying slightly in diameter and degree of spining; they are thicker and have more pronounced spination in the Palau specimens; (b) tylasters, with extremely fine rays usually 5–8 in number; in the Palau specimens forms of these spicules occur which grade toward a chiaster by thickening of the rays and even toward an anthaster by these rays becoming rugose; (c) large anthasters, found only in the Palau specimens, and ranging from two- to eight-rayed forms, the triact being particularly common; (d) tylospherasters found only in the Ifaluk sponges, extremely tiny spicules, 4–6 $\mu$  in diameter, with a pronounced centrum and up to 16 short rays. In this whole complex of sponges asterose microscleres are relatively rare

and in one specimen (Ifaluk 798) almost entirely absent.

DISCUSSION: Burton (1937) has tabulated the salient characters of ten species of *Ecionemia* from the Indo-Pacific area and demonstrates that all can be referred to *Stelletta bacillifera* Carter. At this time Burton presumably considered *Ecionemia acervus* Bowerbank as distinct from *E. bacillifera*; in 1959, however, he extends the synonymy to include *E. acervus*. This later synonymy is not supported by any additional evidence, but since such species as *Ecionemia agglutinans* Thiele and *Ecionemia cribrosa* Thiele had already been included in the broad view of *E. bacillifera* (Burton, 1937), the inclusion of *E. acervus* with its microscleer complement of tylasters, tylospherasters, and microrhabds is not unreasonable. *E. acervus* Bowerbank is very close in spiculation to the

Ifaluk specimens described above; the Palau specimens and the type of *H. walkeri* are inseparable from *S. truncata* Kieschnick and *E. amboinensis* Lendenfeld. Thus, in these two relatively contiguous localities, we have two populations definitely separable on spicule characteristics. Although Burton's propositions with regard to this complex are adopted here, indications are that further study may reveal two and possibly three species grouped under *E. acervus*.

It is not absolutely clear from the literature that *Ecionemia* Bowerbank (1862) is a synonym of *Ancorina* Schmidt (1862). Sollas (1888) made the first significant contribution to our knowledge of these genera and he clearly understood *Ancorina* Schmidt to possess sanidasters and oxyasters, therefore falling into the Sanidasterina, and *Ecionemia* Bowerbank to possess microrhabds and tylasters to spherasters, thus falling into the Rhabasterina.

Sollas did not state the source of his information as to the microscleer spiculation of *Ancorina cerebrum* Schmidt. There are no figures of microscleeres in the type description and reference is made only to "sternchen et kugeln." In the absence of any redescription of Schmidt's material it can only be assumed that Sollas interpreted "kugeln" to mean sanidaster. Dendy (1905, 1916) was aware of the difficulty of separating *Ecionemia* and *Ancorina*, but by 1924 was convinced that sanidasters graded into microrhabds and consequently that *Ecionemia* fell to *Ancorina*. Dendy's conclusion is adopted here, as it is the only clear directive with regard to the relationship of these two genera.

It has been mentioned above that the holotype of *Hezekia walkeri* de Laubenfels contains anthasters and tylasters and certainly belongs to the *Ancorina acervus* complex. The genus *Hezekia* was established by de Laubenfels (1934) for *H. demera* from Puerto Rico. The holotype of the type species (USNM 22206) has been re-examined and found to contain abundant tylospherasters and tylasters, the former 4–6 $\mu$  in diameter with short rays, the latter up to 8 $\mu$  in diameter with 5–7 long fine rays. *Hezekia* de Laubenfels thus falls to *Ancorina* Schmidt; the species *demera* may or may

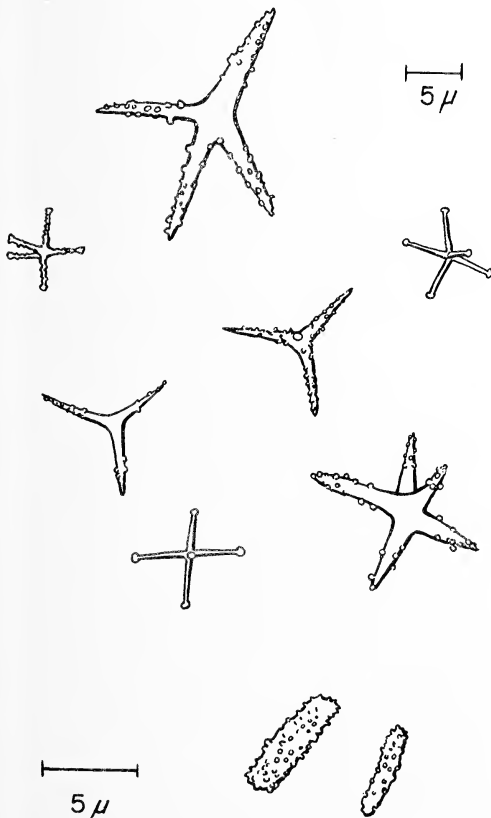


FIG. 31b. *Ancorina acervus* (Bowerbank). Microscleers, drawn from the holotype of *Hezekia walkeri* de Laubenfels.

TABLE 15

SPECIMEN	ENDOSOMAL OXEAS	ORTHOTRIAENES	PROTRAENES (ALWAYS RARE)	ANATRIAENES	CORTICAL OXEAS	MICROHABDS	TYLASTERS	ANTHASTERS
<i>Hezekia walkeri</i> de Laubenfels, USNM 22925 <sup>10</sup>	(1000-2000) × 20-40μ 1800- (2158) - 2625 × 20- (29)-50μ	(sev. thousand × 40μ) 1150- (1529) - 2287 × 23- (35)-43μ	(1000 × 8μ) 1150-2000 × 8-12μ	(1500 × 15μ or less) 1437- (2171) -2500 × 8- (12.5)-15μ	(240 × 4μ) 200- (237)-275; × 1.5-(2.6)- 3.5μ 1.5- (2.6)-3.5μ	(10.1-13) × 1-1.5μ 8.5- (10.5)-14 × 1.5- (1.9)-3μ	6- (9.5) - 13.5μ	12-28μ
220A Palau Spec. 1	1062- (1932) - 2275 × 6.5- (24)-44.5μ	360- (1419) - 2025 × 6- (28)-46μ	1560-1937 × 7-10μ	1837- (2081) -2437 × 10- (13)-15μ	178- (260)-312 × 2- (2.8)-3.5μ	10- (11)-13 × 1- (2)-3.5μ	6- (9.4) - 14μ	14-30μ
220A Palau Spec. 2	1050- (2023) - 2720 × 7.5- (32)-50μ	712- (1726) - 2562 × 23- (35)-46μ	1650 × 12μ	1075- (2067) -2687 × 8- (13)-16.5μ	212- (248)-287 × 2- (3)-3.5μ	7.5- (10)-13.5 × 1.5- (1.9)-2.5μ	6- (9.9) - 14.9μ	14-46μ

<sup>10</sup> Bracketed dimensions are those given in the type description.

not be distinct from previously described members of *Ancorina* from this area.

Lévi (1958) has described a third species in *Hezekia*, *H. arabica*. It is possible that this sponge does lack asters; certainly it differs markedly from *Ancorina acervus* in details of spiculation. If the opinion that lack of asters warrants generic separation is upheld, then *H. arabica* requires a new generic name.

DISTRIBUTION: Wide Indo-Pacific distribution.

GENUS *Stelletta* Schmidt

*Stelletta durissima* n. sp.

Fig. 32

OCCURRENCE: Sta. 64 (a single specimen designated as Holotype, USNM 23704).

DESCRIPTION: A small flattened fragment, 1.0 cm high, 1.2 cm wide, 0.5 cm thick, of what was presumably a simple, digitate sponge. The base of attachment is missing and there is no information as to the substrate.

COLOR: In alcohol, grayish-white.

TEXTURE: Crisp.

SURFACE: Uneven, rough with the slightly projecting clads of the outer layer of triaenes. No oscules are visible, but a lateral pore area of approximately 1.0 × 1.5 mm is present on each side of the sponge. In this area the density of surface triaenes is greatly reduced and the skeletal pores are subdivided irregularly by fine whips of collenchymatous tissue.

SKELETON: The arrangement of the skeleton is typical of *Stelletta*, comprising radially disposed tracts of oxeas, slightly confused internally and diverging toward the surface. There are two ranks of triaenes in both of which plagiotriaenes predominate, although they are accompanied in each case by anatriaenes. The triaenes of the inner rank interdigitate with the endosomal oxeas and are frequently very short plagiotriaenes.

Small cortical oxeas are mingled with the outer rank of triaenes; they are usually radially disposed but can occur scattered between the two triaene zones. The latter are separated by a region of subcortical cavities which marks the boundary between cortex and endosome.

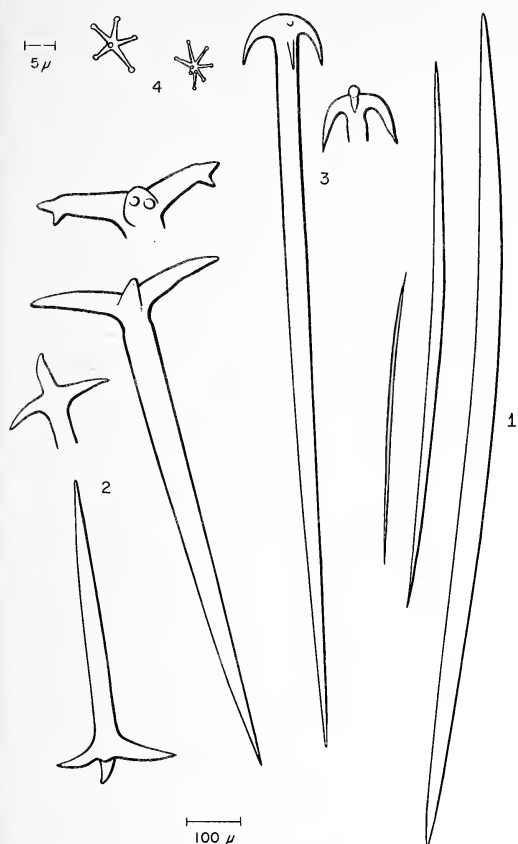


FIG. 32. *Stelletta durissima* n. sp. Sta. 64. Holotype. USNM 23704. Spicules: 1, Oxeas. 2, Plagiotriaenes. 3, Anatriaenes. 4, Tylasters.

Microscleres are distributed sporadically throughout the sponge and are frequent lining the subcortical channels.

**SPICULES:** *Megascleres*. (a) Plagiotriaenes, often tending toward orthotriaenes, with stout shaft tapering abruptly in the posterior third to a stylote or oxeote termination. Many of the larger triaenes are incipient dichotriaenes; the bifurcation of the axial canals in the clads often can be seen, but dichotriaenes are rarely formed. The tips of the clads are often reflexed at an acute angle to the shaft.

Smaller triaenes often have irregular cladomes; four-branched forms are common and occasionally one or two abbreviated clads project from the shaft below the actual head of the spicule. Frequently the angle between clads is unequal, giving the cladome a two-dimensional appearance.

(b) Anatriaenes with strongly recurved and exceedingly stout clads. These spicules rarely have perfect form; the cladome can be slightly subterminal, with the shaft projecting as a nubbin beyond the point from which individual clads diverge, or both the angle between clads and the curvature of the rays may vary greatly on a given spicule.

(c) Oxeas, which are frequently strongly oxeote; these spicules make up the entire endosomal skeleton.

(d) Fine, spindle-shaped cortical oxeas, not sufficiently abundant to form a distinct layer.

*Microscleres*. Tylasters, with 5–10 long fine rays.

**DIMENSIONS:** Plagiotriaenes: 500–(835)–1398  $\times$  19–(38)–70 $\mu$ ; cladome: 60–487 $\mu$ . Anatriaenes: 787–(1134)–1375  $\times$  23–(32)–37 $\mu$ ; cladome: 125–150 $\mu$ . Oxeas: 587–(1009)–1460  $\times$  16–(32)–50 $\mu$ . Cortical oxeas: 200–(223)–240  $\times$  2–(2.8)–4 $\mu$ . Tylasters: 8–(9.7)–10.5 $\mu$ .

**HISTOLOGY:** The cortex is a distinct layer, 125–175 $\mu$  deep, composed of a dense collenchymatous matrix in which spindle-shaped cells are relatively abundant. The inner boundary of this layer is marked by a zone of cells with coarsely granular cytoplasm; these line the roof of subcortical channels but are also dispersed between and below them. The fleshy tissue of the endosome is granular.

**DISCUSSION:** *Stelletta durissima* is closest in spiculation and morphology to *Stelletta clavosa* Ridley and particularly to *S. (Myriastria) clavosa* var. *quadrata* Sollas, which has similar anatriaenes.

The chief differences are that *S. durissima* has incomplete, malformed dichotriaenes where *S. clavosa* has normal dichotriaenes as the surface spicules; plagiotriaenes are present in *S. durissima* and absent from *S. clavosa*; anatriaenes are often irregular in form in *S. durissima* and all megascleres are substantially shorter and stouter in this species than in *S. clavosa*. The single, circular, depressed osculum described for *S. clavosa* by all authors has not been observed in *S. durissima*. The latter is further distinguished by the presence of a double layer of triaenes.

The decision taken by Dendy (1905) and de Laubenfels (1936) to separate *Stelletta*

Schmidt and *Myriastr*a Sollas on the grounds that species of *Myriastr*a possess only one type of aster, a chiaster or tylaster, was admittedly arbitrary; the opposite view has been taken by Burton (1926). It is not consistent to limit stellettid genera by the possession of a single and widespread type of aster. Species such as *Myriastr*a *debilis* Thiele have only oxyasters. Such a sponge is not, in Dendy's view, a *Myriastr*a. If the generic diagnosis is to be widened to admit it, then the argument that a genus can be limited by the possession of a single microscle category when a closely related genus exhibits a variety of microscles, including this type, obviously cannot be upheld. It would lead to the establishment of individual genera for every stellettid with only one type of microscle. Both tylasters and oxyasters are common among species which have been referred to *Stelletta* and it is preferred here, following Burton, to regard all species possessing only a single microscle category as belonging to this genus.

#### FAMILY TETILLIDAE Sollas

#### GENUS *Tetilla* Schmidt

#### *Tetilla microxea* n. sp.

Fig. 33a, b

OCCURRENCE: Sta. 53 (one specimen, the Holotype, USNM 23700).

DESCRIPTION: A small, hemispherical sponge growing upon a coral fragment; unfortunately

the specimen is damaged and approximately half remains attached. The characteristic feature of the specimen is the presence of long projecting surface spines each made up of one to twelve stout oxeas.

The sponge is 1.9 cm high, 1.6 cm wide, and the surface spines range from 2.5 to 7.0 mm. Basal rooting tufts, frequently well-developed in species of *Tetilla*, are only just indicated at the base of this specimen.

COLOR: In alcohol, reddish-brown (YR 5/4) externally, pale brown internally (approximately yY-R 7/4).

TEXTURE: Firm, compressible.

SURFACE: Conulose, spiny, and granular. Each projecting radial tract raises the skin-like ectosome into a marked conule and the tissue surrounding the spicules may extend up to 2.5 mm beyond the level of the sponge surface. Conules are spaced relatively regularly over the surface, approximately 1–3 mm apart. The actual surface tissue of the sponge appears granular, contains abundant sigmas and microxeas, and has a considerable amount of detritus and large foraminiferans adhering to it. No pores or oscules are apparent.

SKELTON: Tracts of large oxeas radiate from the center of the sponge to the surface; occasional megascleres occur between these tracts but the predominant spicules in this position are microxeas. Both protriaenes and anatriaenes are present in addition to the oxeas in the endosomal skeleton; these spicules are, however, extremely rare. There is no layer of radially disposed cortical oxeas and no special disposition of the triaenes. The sigmaspirae are extremely abundant in the dermal region and in the outer half of the endosome; microxeas have a similar distribution.

SPICULES: *Megascleres*. (a) Oxeas, large straight spicules frequently stair-stepped, tapering to sharp points. (b) Anatriaenes, with flattened cladome, very slightly recurved rays and long lash-like rhabdome. These spicules are rare overall but seem to occur in groups associated with the endosomal oxeas, not, as in many retillids, concentrated toward the base of the sponge. (c) Prottriaenes. Only two spicules were found, one with stout straight shaft and irregular cladi, the other a fine prodiaene, with

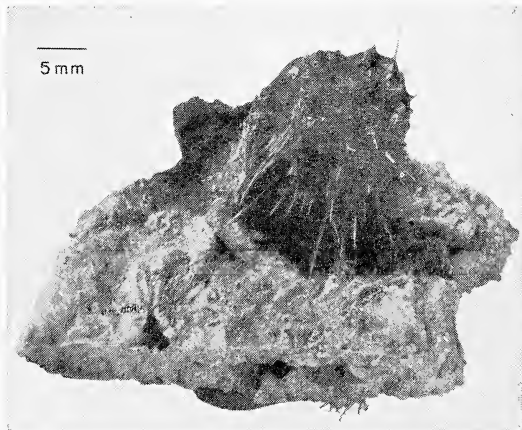


FIG. 33a. *Tetilla microxea* n. sp. Sta. 53. Holotype. USNM 23700.

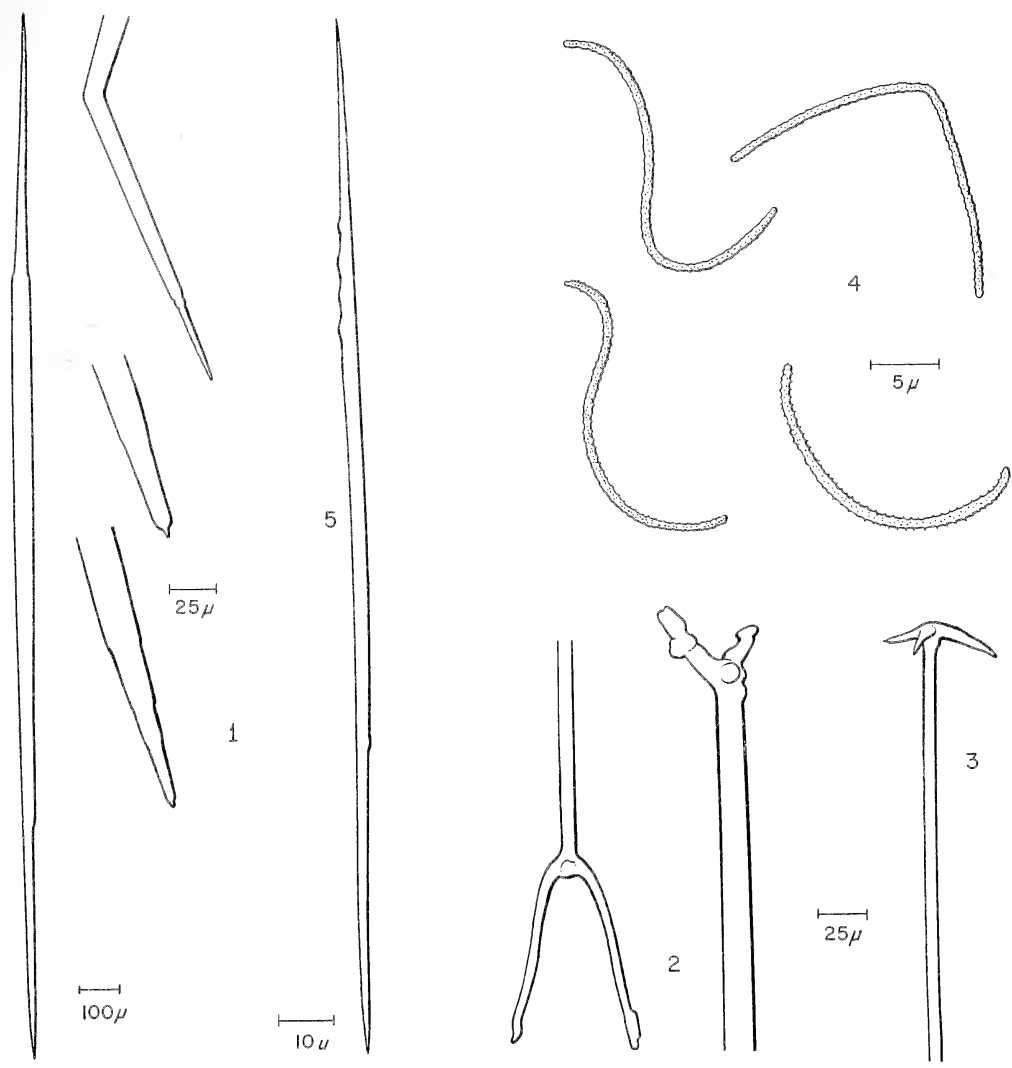


FIG. 33b. *Tetilla microxea* n. sp. Spicules: 1, Oxeas. 2, Prodiaenes. 3, Anatriaene. 4, Sigmaspirae. 5, Microxea.

the cladome head just below the sponge surface.

**Microscleres.** (a) Microxeas, fine, spindle-shaped spicules which are distributed tangentially in the dermis and in confusion in the endosome. (b) Sigmaspirae of typical tetillid form but apparently quite smooth.

*Spicule dimensions* (in  $\mu$ ).

Oxeas:  $587-(2000)-2875 \times 4-(30)-50$ .  
Anatriaenes: at least  $3400 \times 3-8$  (all spicules incomplete), cladome 33. Protriaenes:  $3125 \times 8.5$  cladi,  $16-40 \times 2.5-3.5$ , cladome  $13-50$ .  
Microxeas:  $150-(184)-230 \times 1.5-(2.3)-3.5$ .  
Sigmas:  $10-(18)-32$ .

**HISTOLOGY:** The ectosome is not a clearly differentiated region; the dermis is a slightly collenchymatous, lightly pigmented layer which grades imperceptibly into the endosomal sarcoenchyma.

**DISCUSSION:** *Tetilla microxea* can be compared with *Tetilla monodi* Burton from West Africa and *Tetilla oxeata* Burton from south Arabia. These three species are, as far as can be ascertained, the only other members of this genus which possess small oxeas and have them scattered throughout the sponge rather than arranged in a definite cortical layer. *Tetilla*



*microxea* differs from *T. monodi* and *T. oxcata* in that the supplementary oxeas are small and have the same distribution as the microscleres, in the great rarity of triaenes, and in details of body shape, color, and surface. *Tetilla rubra* Kieschnick differs in lacking the spiny surface, in having abundant triaenes and in having calthrops in the basal rooting tufts, the latter characteristic suggesting that this species belongs in *Paratetilla*.

The genus *Tetilla* is understood here in the sense of Sollas (1888) and Wilson (1925). The synonymy of *Craniella* Schmidt with *Tetilla* Schmidt has not been satisfactorily demonstrated, neither have good reasons been produced to uphold the use of two separate families, Craniellidae and Tetillidae as de Laubenfels (1936) proposed.

#### GENUS *Paratetilla* Dendy

*Paratetilla bacca* (Selenka)

Fig. 34

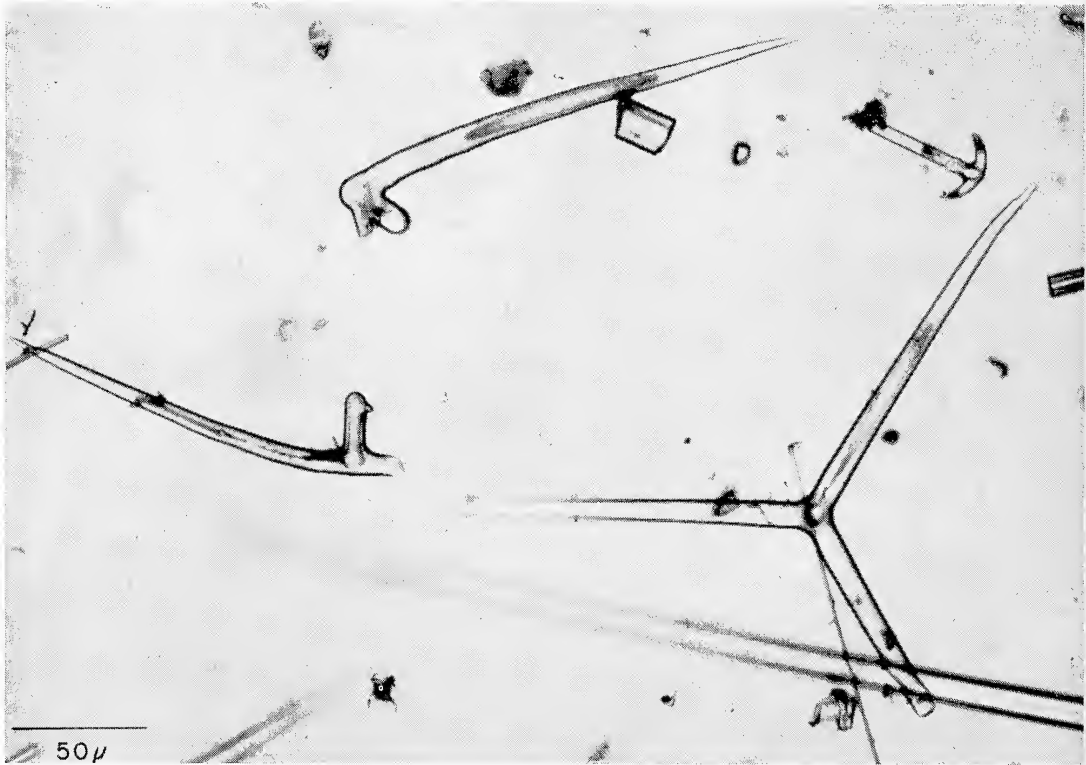


FIG. 34. *Paratetilla bacca* (Selenka). Sta. 47. Malformed orthotriaenes.

#### RESTRICTED SYNONYMY:

*Stelletta bacca* Selenka, 1867, p. 569, pl. 35, fig. 14, 15.

*Tethya merguiensis* Carter, 1883, p. 366, pl. 15, figs. 6-8.

non *Tetilla merguiensis* Topsent, 1897, p. 437.

*Tetilla bacca* Lindgren, 1898, p. 328.

*Paratetilla bacca* Dendy, 1905, p. 97.

*Paratetilla bacca* Dendy, 1921, p. 21.

*Paratetilla bacca* Kumar, 1925, p. 217.

*Paratetilla bacca* Burton, 1959, p. 200.

OCCURRENCE: Sta. 47.

DISCUSSION: The single specimen in this collection is extremely close to *Paratetilla cineriformis* Dendy from Ceylon and *P. eccentrica* Row from the Red Sea in features of general morphology and spiculation. Dendy (1921) has referred *P. cineriformis*, with many other forms, to *P. (Stelletta) bacca* Selenka and there is little that need be said to supplement his work. Those points which can be criticized have been dealt with by Wilson (1925). It is

agreed that the removal of *Tetilla merguiensis* Topsent 1897 to *Amphitetthya* as suggested by Wilson is desirable, but Dendy's view as to the presence of poriferous pits in *Stelletta bacca* Selenka is well reasoned and is upheld. Further, Wilson questions the synonymy of *P. eccentrica* Row with *P. bacca*, claiming that the great irregularity of the triaenes justifies the separation of this species. Malformed triaenes are the rule in the Palau specimen and all modifications described by Row for *P. eccentrica* can be observed. *P. cineriformis* Dendy also possesses malformed triaenes. In view of this the separation of *P. eccentrica* cannot be maintained. The status of *Paratetilla lipotriaena* de Laubenfels (1954:244) is uncertain. The holotype (USNM 23049) has been re-examined and has been found to possess occasional prodiaenes, promonaenes, and anatriaenes with reduced rays. The calthrops or orthotriaenes are identical with those of the specimen assigned here to *P. bacca*; other skeletal elements, color, and general morphology also agree with the Palau specimen. In view of the abundance of triaenes in my specimen and their scarcity and reduced form in *P. lipotriaena*, this species is retained as a valid one for the present.

DISTRIBUTION: Indian Ocean and western Pacific.

#### GENUS *Cinachyra* Sollas

*Cinachyra australiensis* (Carter) (complex of species)

RESTRICTED SYNONYMY (for extensive synonymy refer to Burton, 1934):

*Tethya cranium* var. *australiensis* Carter, 1886, p. 127.

*Cinachyra australiensis* Burton, 1934, p. 523.

*Cinachyra australiensis* de Laubenfels, 1954, p. 242, fig. 166.

OCCURRENCE: Sta. 47, 125, 200 (2 specimens).

DISCUSSION: The four hemispherical specimens in the collection are not identical in spiculation but are very similar in external form. There is variation in the size and degree of torsion of the sigmaspires, those in specimen Sta. 47 being small and tightly curved while

those of the remainder are larger and more open. Microxeas are variable in their number and degree of spination; they are rare and occasionally roughened in the specimen from Sta. 220, relatively abundant and roughened in that from Sta. 125, relatively abundant and smooth in that from Sta. 47.

Prottriaenes and anatriaenes are present in all specimens.

DISTRIBUTION: Australia, Malay area, Indian Ocean.

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# A New Species of *Pachycerianthus*, with a Discussion of the Genus and an Appended Glossary<sup>1</sup>

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**ABSTRACT:** A new species of *Pachycerianthus* from southern California is described and the status of the genus is discussed. A glossary of the terms used in the taxonomy of the order is appended.

THE ORDER Ceriantharia consists of long, solitary, anemone-like Anthozoa, without a pedal disc or external skeleton, with numerous single tentacles in two crowns, coupled mesenteries, and a single siphonoglyph. Earlier authors related these anemones to the Actiniaria, but they are recognized by recent authors, such as Wells and Hill (1956), as being most closely related to the Antipatharia or "black corals."

Previous knowledge of the taxonomy and morphology of the Californian Ceriantharia is meagre. McMurrich (1893:202-203) described a species, *Cerianthus vas*, from one poorly preserved specimen that had been collected at Isla de Cedros, Baja California, Mexico. The whereabouts of this specimen is unknown and the information given is insufficient to allow identification of the species or to place it in any recent genus or family. Torrey and Kleeberger (1909) described three species: *Cerianthus aestuari*, *C. benedeni*, and *C. johnsoni*, basing their descriptions on animals collected from Mission Bay, San Diego Bay, and San Pedro Harbor, California, respectively. The description of the latter species was based on two specimens. Although these descriptions were incomplete, enough morphological data were given so that McMurrich (1910:11) placed *Cerianthus benedeni* in the genus *Botruanthus*, which he erected for it. He placed the other two species in the genus *Pachycerianthus* Roule. Carlgren (1951:433-436) described *Pachycerianthus insignis* from a single incom-

plete specimen, and redescribed *Botruanthus benedeni* from four specimens, all taken from the Gulf of California.

Child (1908) reported on regeneration in *Pachycerianthus aestuari*. Other authors have referred to forms collected in California, but have not identified them. When specimens were obtained by divers near Los Angeles it was found that they belonged to previously undescribed species. One of these species is described here with a discussion of the genus *Pachycerianthus* in which it is placed.

As indicated by Torelli (1960:373), the terminology used for the various anatomical structures in the Ceriantharia is greatly confused in the literature. A glossary of terms used in the taxonomy of this group is therefore appended, and the terminology used throughout this work has been standardized for uniformity.

## MATERIAL AND METHODS

The sea anemones on which the anatomical descriptions are based were collected by Dr. Rimond Fay and Mr. Philip Bernard of the Pacific Bio-marine Supply Company between July, 1958 and August, 1960 and were maintained in the sea water tanks of the Department of Zoology, University of California at Los Angeles. On removal from the tanks, the animals were anaesthetized for 2-8 hours in equal parts of sea water and a solution of 0.36M  $MgCl_2 \cdot 6H_2O$ . They were fixed for approximately 15 minutes in 10% neutral formalin (with an excess of  $MgCO_3$ ), overnight in picro-formol solution (one part concentrated formalin: 3 parts saturated picric acid), and stored in 70% ethanol. In each case the solutions were pipetted into the coelenteron.

Preliminary identification of nematocyst types was done on fresh material. The nematocyst

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measurements given in this section were obtained from portions of five of the paratypes of the species sectioned and stained with Heidenhain's iron hematoxylin and eosin, Mallory's triple stain, and acid haemalum and light green. Ten nematocysts of each type were measured in each portion of each animal examined.

## RESULTS AND DISCUSSION

### Family CERIANTHIDAE

DIAGNOSIS: Ceriantharia without acontiods or cnidorages.

Genus *Pachycerianthus* Roule, 1904.

DIAGNOSIS: Cerianthidae with the second couple of protomesenteries short and sterile. Arrangement of metamesenteries in each quartette M,B,m,b (1,3,2,4) more or less distinct.

### DISCUSSION

Torelli (1961:25-27) claims that the genus *Pachycerianthus* proposed by Roule (1904a: 792-793) is invalid since it is not clearly distinguished from the genus *Cerianthus*. Her opinion is partly based on an incorrect interpretation of the terms in the literature. It is therefore first necessary to trace briefly the history of some of the terms used to describe the mesenterial filaments and their appendages.

Haime (1854:374) noted the presence of "cordons pelotonnes" along the edge of some of the mesenteries of *Cerianthus membranaceus*. Von Heider (1879:216-217) and Hertwig and Hertwig (1879:578-580) described the "Mesenterial-filamente" of the same species in more detail. The mesenteries of this species have numerous branching appendages, the "Mesenterialfaden," which are not homologous to the acontia of the Actiniaria (as von Heider thought), since they possess ascending and descending limbs of the mesenterial filament separated by a portion of endoderm. Van Beneden (1897:27-37) further investigated the structure of the "filaments mésentériques," or "craspedes" of Gosse (1860:xxiii) in specimens of several adult and larval species. He found "fils mésentérique" with a structure similar to Hertwig and Hertwig's "Mesenterial-faden" and also, in several larval species, much

longer and rounder appendages near the posterior end of the mesentery which he believed to be true "acontie." McMurrich (1910:19) used the term "craspedoneme" to distinguish Hertwig and Hertwig's "Mesenterialfaden" from these "acontia."

Carlgren (1912a:68-72; 1912b:383-385), re-investigating the same species examined by van Beneden, showed that true acontia were not present even there but rather structures homologous with the craspedonemes were present in which the endoderm was reduced so as to be surrounded by the two limbs of the filament. Bourne (1919:60-61) also noted differences between the "acontia" of Ceriantharia and those of the Actiniaria. In some portions of the collected works of van Beneden published posthumously in 1923, the term "acontie" is used. However, in another portion he, in agreement with the above authors, also states that the Ceriantharian structures are not homologous with those of the Actiniaria. Carlgren suggested the term "mucocraspedoneme" for the structures found in the Ceriantharia, but in later papers adopted the term "acontiod" introduced by Pax (1914:394).

With this background, no purpose was served by Torelli's statement (1960:376-379) that acontia are not present in Ceriantharia, especially since her opinion was based on an investigation of two species for which previous authors had not even claimed the presence of acontiods, i.e., *Cerianthus membranaceus* and *Pachycerianthus dohrni* (the *Cerianthus viridis* of her paper).

We may now consider the description of *Pachycerianthus*. Roule (1904a: 792-793; 1904b:708-710) described *Pachycerianthus benedeni* and designated it the type of the genus. The description is poor but includes the following characters of possible generic significance:

1. Mesenteries are short; only the ventral mesenteries ( $S_3$  in the terminology proposed by van Beneden) reach the aboral extremity and border a narrow band which continues the sulcus and contains the vestiges of the D and  $S_1$  mesenteries.

2. The mesenteries on either side of the  $S_3$  diminish in length toward the dorsal region but do not show a distinct quatro-septal dispo-

sition; the irregular diminution gives them, rather, a biseptal arrangement.

3. All the mesenteries, except those which occupy exactly the dorsal region, possess some "craspedes" in the zone placed immediately below the enterostome. Some mesenteries have "fils mésentériques" on their "craspedes," and alternating ones do not carry them. The mesenteries deprived of "fils mésentériques" are fertile and possess "aconties" on a rather large part of their inferior extremity; their series begins with the  $S_3$  and continues with the uneven numbered mesenteries  $S_5$ ,  $S_7$ ,  $S_9$ , etc.

As Torelli (1961:25–27) pointed out, this description is extremely incomplete, and hence it is very difficult to place the genus in the modern classification of the order. Some of her comments (1960:374–375; 1961:25) about the lack of clarity can be discounted, however, since she has translated incorrectly the term "fils mésentériques" in the third item above as mesenterial filaments. As noted earlier the term was used by van Beneden (1897:33) and other French authors to refer rather to the "Mesenterialfaden" or craspedonemes. Correctly translated, the third passage states that some mesenteries have craspedonemes on their "craspedes" or mesenterial filaments and alternate mesenteries have "aconties" on them.

It is the interpretation of the term "aconties" in the third passage above that is most problematical. McMurrich (1910:10–14, 22–24), in his classification of the order, placed the genus in a family characterized by the presence in the larva of "acontia" or, as they were later called, acontiods, but included adult species both with and without acontiods. Carlgren (1912a:37–48) believed that the structures must be ordinary craspedonemes since acontiods in all the better known species are single, rather than scattered over a large part of the lower end of the mesentery. He placed the genus in the family Cerianthidae characterized by the lack of both acontiods and cnid-orages. Although Carlgren is probably correct, the question can only be resolved definitely by reference to the type specimen; unfortunately the location of this material is at present unknown. In the meantime we may assume, as Torelli (1961:26) also does, although for the

wrong reason, that these appendages are ordinary craspedonemes. *Pachycerianthus* is therefore retained in the Cerianthidae.

Without re-examination of the original material, Carlgren (1912a:40–48) defined the genus *Pachycerianthus* as "Cerianthidae whose second couple of protocnemes are short, sterile, and provided with an extremely well-developed region of the cnido-glandular tract. Arrangement of the metacnemes (=deuteroconemes McMurrich) in each quartette M,B,m,b (1,3,2,4) more or less distinct." He originally included eight species in the genus and later (1924a:182–186; 1940:15; and 1951:435–436) added three more. All of these species (even *P. benedeni*, if we are considering the first quartette) have M,B,m,b metamesenterial arrangement. All except *P. benedeni* are known to have short, sterile second protomesenteries, and it is probable that in that species they are also sterile since very small mesenteries are rarely fertile. However, Carlgren has placed in the genus several species (including *P. benedeni*) in which the extent of the cnido-glandular tract is unknown, and also others, such as *P. maua*, in which it is very short. In addition, as Torelli (1960:375–376) has indicated, the distinctness of the histological demarcation by Carlgren (1912a:59–67) of the mononeme into the cnido-glandular tract and the craspedion is questionable. (The mononeme is the aboral monofilar portion of the mesenterial filament.) It seems desirable therefore that this character be eliminated as a differential one not only in this but in all genera of cerianthids.

The 10 species (other than *P. benedeni*) placed in the genus by Carlgren comprise a distinct taxonomic entity with the remaining characters with which Carlgren defined *Pachycerianthus* and with no acontiods. *C. bicyclus* Torelli, 1961 and *P. torreyi* n.sp. of the present work may also be added. This group is separated from the genera *Cerianthus*, *Ceriantheopsis*, and *Ceriantheomorphe* by the possession of short, sterile second protomesenteries, and from *Ceriantheopsis* by the MBmb arrangement of the metamesenteries in *Pachycerianthus*. Torelli (1961:27) does not believe that the properties of the second protomesenteries

are important enough to serve as generic characters or to distinguish *Pachycerianthus* from *Cerianthus*. These mesenteries, however, are the first couple of mesenteries to develop and could therefore be expected to be the most stable in the grown animal. McMurrich (1910: 23-24) considered the form of these mesenteries to be characteristic, even at the familial level.

In summary, it should be stated that an intensive search must be made for the type specimen of *P. benedeni*. It is not in the collections of the Musée Océanographique de Monaco, the Musée de Bruxelles, the British Museum (Natural History), or the Museum National d'Histoire Naturelle, Paris, the most likely repositories. If it cannot be found, it will be necessary to declare the species a *nomen dubium*. Since the other twelve species presently included in the genus appear to constitute a taxonomic entity, the declaration of the *nomen dubium* would necessitate selection of a new type species and generic name for the taxon. In the meantime, *Pachycerianthus* is retained in the Cerianthidae and includes the following species: *P. aestuarii* (Torrey and Kleeberger, 1909); *P. benedeni* Roule, 1904; *P. bicyclus* (Torelli, 1961) n. comb.; *P. dohrni* (van Beneden, 1923); *P. fimbriatus* McMurrich, 1910; *P. insignis* Carlgren, 1951; *P. johnsoni* (Torrey and Kleeberger, 1909); *P. maua* (Cargren, 1900); *P. monostichus* McMurrich, 1910; *P. multiplicatus* Carlgren, 1912; *P. plicatus* Carlgren, 1924; *P. solitarius* (Rapp, 1829); and *P. torreyi* n. sp.

*Pachycerianthus bicyclus* is distinguished from all other members of the genus by having two cycles of marginal tentacles but three or four cycles of labial tentacles, and lacking craspedonemes but possessing aboral appendices on the second protomesenteries and first order metamesenteries. Torelli (1961:24-25) states that the specimens from which *P. bicyclus* was described may not have reached full growth, so that the species may prove to be an immature stage of another. Since *P. solitarius* from the same area differs only in the number of cycles of marginal tentacles, these species will probably prove to be synonymous.

### *Pachycerianthus torreyi* n. sp.

**DIAGNOSIS:** Siphonoglyph running length of actinopharynx. Directive mesenteries extending well beyond siphonoglyph. Second protomesenteries between once and twice length of directives. Metamesenteries having definite MBmb arrangement.  $M_1$  definitely longer than any other mesentery.  $M_3$  longer than  $M_2$ .  $m_2$  and  $m_3$  shorter than  $m_1$ .  $B_1$  shorter than  $P_3$ .  $M_1$  with trineme almost to end of mesentery, craspedonemes scattered over most of its length, very short or no mononeme.

**LOCALITIES:** Latigo Cove; and just inside breakwater, Los Angeles Harbor (type locality), California.

**HABITAT:** 12-18 meter depth; in mud, or mixed gravel and mud, bottom.

**HOLOTYPE and PARATYPES:** To be deposited in USNM.

**DESCRIPTION** (based on 10 adult specimens):

*Coloration of live animals.* Column red-brown, darkest just below oral disc and toward aboral pore, with narrow buff ring immediately around aboral pore. Marginal tentacles buff (shading to bright pink towards tips in one specimen). Oral tentacles darker, with purplish tinge.

*Coloration of animals fixed in picro-formol.* Red pigments of live animals faded, leaving column light yellow-brown, tentacles yellowish buff.

*Length in anaesthetic.* 13-31 cm (type 18.5 cm).

*Tentacles.* Marginal arrangement 2(dt)431.4231.4231... Labial arrangement 2(dt)313.4232.4312... or 3(dt)413.4232.4312... (type). In each crown division into third and fourth cycles indistinct in some specimens. Directive labial tentacle present. Marginal tentacle number approximately 90-125 (type approximately 100).

*Siphonoglyph.* Running length of actinopharynx. Attached mesenteries 10 (type) or 12. Hyposulcus indistinct, less than one-tenth length of siphonoglyph. Hemisulcus distinct, flat orally, continued down directive mesentery as a filament without ciliated tracts.

**Protomesenteries.** Directive mesenteries shorter or longer (type) than siphonoglyph. Second protomesenteries sterile, less than twice length of directive mesenteries, with aboral lobe varying greatly in length (long in type), trineme running to near tip of aboral lobe, usually (type) with several craspedonemes at aboral end of trineme, convoluted mononeme running around tip of lobe. Third protomesenteries sterile, approximately same length (type) or shorter than  $P_2$ , longer than  $P_1$ , trineme much shorter than in  $P_2$  with a number of craspedonemes at aboral end, mononeme relatively long and highly convoluted along border of broad section of mesentery.

**Metamesenteries.** Definite MBmb arrangement (Fig. 1). Reproductive organs in macrosepta only.  $M_1$  mesenteries at least five-sixths length of column, never reaching aboral pore; remaining mesenteries less than two-thirds length of  $M_1$  in most specimens (longest mesentery approximately seven-eighths of  $M_1$  in one specimen). Macrosepta generally decreasing in length toward multiplication chamber;  $M_3$  longer than  $M_2$ ,  $m_2$  and  $m_3$  shorter than  $m_1$ ,  $m_3$  longer or shorter (type) than  $m_2$ .  $M_1$  with trineme almost to aboral end of mesentery, craspedonemes scattered over most of its length, sometimes with an aboral lobe of mesentery or bunch of craspedonemes at aboral end of trineme, short mononeme (type) or none, reproductive region to above level of craspedonemes, hermaphroditic. Macroseptum  $m_1$  with long trineme terminating much farther from aboral end than in  $M_1$ , trineme with scattered craspedonemes and sometimes with an aboral bunch, mononeme well developed, convoluted or straight (slightly convoluted in type). Extent and form of trinemes and mononemes of other macrosepta variable.  $B_1$  shorter than  $P_3$ , with short trineme with bunch of craspedonemes at aboral end, highly convoluted mononeme along broad section of mesentery. Other B and b with structure similar to  $B_1$  although bunch of craspedonemes of trineme may be reduced or absent.

**Nematocysts** (based on five adult specimens). Of column, atrichs  $29.6\text{--}83.2 \times 5.0\text{--}29.6 \mu$  very common, microbasic b-mastigophores  $18.5\text{--}43.2 \times 3.2\text{--}8.0 \mu$  scarce, holotrichs  $42.2\text{--}67.6$

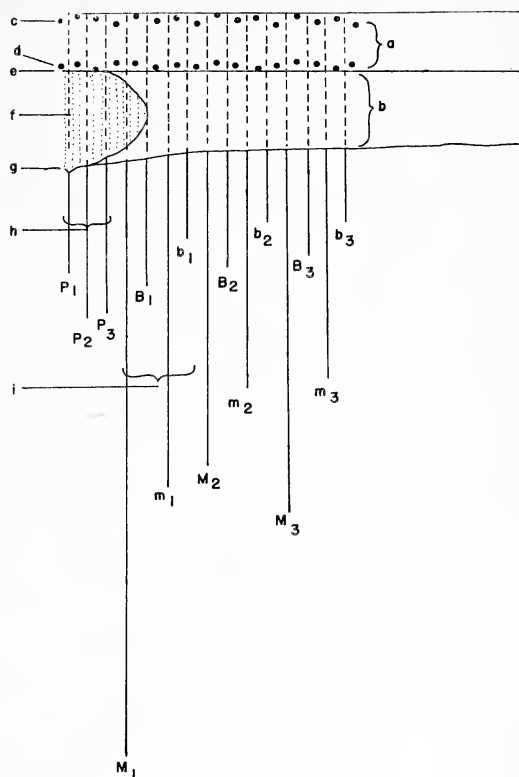


FIG. 1. Diagram of the internal arrangement of *Pachycerianthus torreyi*. View of half the animal cut longitudinally and pinned flat. Approximately  $\frac{1}{2} \times$  vertically,  $5\frac{1}{2} \times$  horizontally. a, Oral disc; b, actinopharynx; c, marginal tentacle bases; d, labial tentacle bases; e, mouth; f, siphonoglyph; g, hemisulcus; h, protomesenteries; i, first quartette of metamesenteries;  $P_1$ , directive mesentery;  $P_2$ , second protomesentery;  $P_3$ , third protomesentery;  $M_1$ ,  $M_2$ ,  $M_3$ , first order metamesenteries;  $m_1$ ,  $m_2$ ,  $m_3$ , second order metamesenteries;  $B_1$ ,  $B_2$ ,  $B_3$ , third order metamesenteries;  $b_1$ ,  $b_2$ ,  $b_3$ , fourth order metamesenteries.

$\times 10.0\text{--}16.2 \mu$  rare. Of marginal tentacles, atrichs  $24.0\text{--}36.8 \times 4.0\text{--}7.2 \mu$  scarce, microbasic b-mastigophores  $20.0\text{--}49.6 \times 3.0\text{--}9.0 \mu$  common, spirocysts  $7.6\text{--}43.2 \times 1.2\text{--}5.6 \mu$  numerous. Of labial tentacles, atrichs  $24.0\text{--}33.6 \times 3.6\text{--}6.4 \mu$  scarce, microbasic b-mastigophores  $19.2\text{--}45.2 \times 2.0\text{--}8.4 \mu$  common, spirocysts  $13.2\text{--}33.6 \times 1.2\text{--}5.2 \mu$  numerous. Of actinopharynx, atrichs  $24.8\text{--}40.8 \times 3.6\text{--}6.4 \mu$  scarce, microbasic b-mastigophores  $20.8\text{--}44.4 \times 2.8\text{--}7.6 \mu$  common, spirocysts  $11.2\text{--}26.8 \times 1.6\text{--}4.4 \mu$  very rare. Of ciliated tract of macroseptum,

atrachs  $21.2\text{--}32.8 \times 2.4\text{--}4.4 \mu$  rare or absent, microbasic b-mastigophores  $18.4\text{--}50.8 \times 2.8\text{--}9.2 \mu$  scarce, spirocysts  $14.4\text{--}26.8 \times 1.8\text{--}5.2 \mu$  common. Of peloton of microseptum, microbasic b-mastigophores  $18.4\text{--}30.0 \times 4.4\text{--}7.6 \mu$  very common.

*Pachycerianthus torreyi* is clearly distinguished from the two species described by Torrey and Kleeberger (1909) from southern California. The present species and *P. aestuari* differ in that the latter possesses a siphonoglyph which does not reach the lips of the actinopharynx and has four mesenteries commonly reaching the terminal pore. Other characters of *P. aestuari* which may differentiate it from *P. torreyi* are a tentacle number which never exceeds 34, a single cycle of marginal tentacles, and a very broad siphonoglyph.

*Pachycerianthus johnsoni* differs from *P. torreyi* in that the directive mesenteries do not extend beyond the siphonoglyph, as is the case in the present species. Other characters of *P. johnsoni* with possible diagnostic value are that gonads are frequently borne on the third order mesenteries, that the siphonoglyph is narrow, and that the  $B_1$  may be longer than the  $P_3$ . Among approximately one hundred cerianthid specimens taken and examined from deeper water in Los Angeles Harbor, the type locality for *P. johnsoni*, no specimens of this species were found. It is probable that it is a shallow water species and that the mud-flat habitat where the two specimens were collected has been eliminated by harbor installations.

The clarity with which the present species can be distinguished from the other species included in the genus depends, in good part, on the detail in which they have been described. We have seen that the type species, *P. benedeni*, was very poorly described, but it is possible to distinguish it since there is a regular diminution in the length of the metamesenteries, i.e.  $M_3$  is shorter than  $M_2$ . *Pachycerianthus insignis*, based on a single incomplete specimen from the Gulf of California, has several metamesenteries almost reaching the aboral pore, and a  $P_2$  that is more than twice the length of  $P_1$ .

*Pachycerianthus torreyi* is most similar to *P. plicatus*, an Indonesian species, differing

only in the relative lengths of the  $M_2$  and  $M_3$  mesenteries. *Pachycerianthus fimbriatus*, from the same area as *P. plicatus*, differs in the same character and possibly in the arrangement of the labial tentacles. *Pachycerianthus bicyclus* and *P. solitarius* differ from *P. torreyi* in the absence of craspedonemes of the trineme and in that several M mesenteries nearly reach the aboral pore. The latter character may also be used to distinguish *P. monostichus*, *P. dobrni*, and *P. multiplicatus* from the present species. *Pachycerianthus maua* differs by having the  $M_3$  mesentery shorter than the  $M_2$ , and also by possessing an unusual type of aboral craspedoneme.

The name, *torreyi*, is in honor of Dr. H. B. Torrey, one of the earliest workers on ceriantharian taxonomy in California.

#### GLOSSARY

As Torelli (1960:373) has pointed out, the terminology applied to the Ceriantharia has become exceedingly complicated through the multiplication of terms. In the following glossary the full definition of a structure has been placed with the presently accepted term and other terms have been referred to this definition. English nomenclature or anglicised terms are used. Terms have been added from other languages where these are not direct translations. The application of certain terms to related groups of animals has been given when they are likely to cause confusion.

- 1 (metamesentery) (Carlgren, 1912b:368)—longest metamesentery in each quartette, i.e. metamesentery of the first order.
- 1 (tentacle) (Carlgren, 1900:25–26; McMurrich, 1910:17–18)—tentacle of innermost cycle of a crown.
- 1 *subscript* (metamesentery) (Carlgren, 1924a:169–170)—belonging to first metamesenterial quartette (*q. v.*).
- 1 *subscript* (protomesentery) (Carlgren, 1912a:12)—belonging to first protomesenterial couple.
- 1 *superscript* (Beneden, 1923:24–25)—closest structure to siphonoglyph in metasome (*q. v.*).
- 1d *superscript* (Beneden, 1897:10–11)—first structure to right with reference to directive plane at the siphonoglyph.

*1g superscript* (Beneden, 1897:10–11)—first structure to left with reference to directive plane at siphonoglyph.

*a superscript* (Beneden, 1923:23)—belonging to second somatome of the prosome (*q. v.*).

*Acontiod* (Pax, 1914:394)—long threadlike, simple or slightly branched craspedoneme, rounded in cross section, with many mucous cells and reduced endoderm, at or near aboral end of mesenterial filament.

*Acontium* (Gosse, 1858:125; 1860:xxiii–xxv, 5; Hertwig and Hertwig, 1879:562–565; Torelli, 1960:376–379) — thin threadlike structure of Actiniaria containing numerous nematocysts, attached at one end to a mesentery, usually below the filament.

*Acontium* (Beneden, 1897:30–33; Bourne, 1919:60–61; Carlgren, 1912a:42, 68–72)—acontiod (*q. v.*).

*Acontium* (Heider, 1879:217)—craspedoneme (*q. v.*).

*Acromere* (Beneden, 1923:22)—“segment” of body, including the directive chamber, directive mesenteries and directive tentacles (by analogy to *Amphioxus*).

*Actinocoel* (Bourne, 1919:35)—intermesenterial chamber (*q. v.*).

*Actinopharynx* (Beneden, 1897:13–14)—tube leading from mouth into coelenteron, lined by longitudinally ridged, invaginated, ectoderm which is supported by mesogloea.

*Actinostome* (Beneden, 1897:9–10, 13–14)—mouth (*q. v.*).

*Animal length*—external distance from base of marginal tentacles to aboral pore.

*Armature* (Weill, 1930:147; 1934:21–22)—spines on tube of nematocyst.

*Arrick* (Weill, 1930:146; 1934:37, 50–52, 624–626)—nematocyst with isodiametric, unarmed, tube open at tip.

*Axenteron* (Beneden, 1897:20)—central portion of coelenteron undivided by mesenteries.

*Axial body* (Moebius, 1866:387; Weill, 1934:22–24)—straight basal section of nematocyst tube within the capsule.

*b* (McMurrich, 1910:14–15)—shorter brachyneme, i.e. microseptum, of a metamesenterial quartette.

*B* (McMurrich, 1910:14–15)—longer brachy-

neme, i.e. microseptum, of a metamesenterial quartette.

*Biseptum* (Beneden, 1897:23)—two longest or two shortest mesenteries of a metamesenterial quartette.

*b-mastigophore* (Carlgren, 1940:3–4)—mastigophore with shaft tapering gradually to terminal tube.

*Botrucnid* (Beneden, 1897:32; Carlgren, 1912a:72–74)—stalked bunch of cnidorages (*q. v.*).

*Brachyneme* (McMurrich, 1910:14)—microseptum (*q. v.*).

*Buccal cone* (Beneden, 1897:9)—raised portion of oral disc immediately surrounding mouth of some larval forms.

*Buccal disc* (Vogt, 1888:29)—oral disc (*q. v.*).

*Buccal tentacle* (Vogt, 1888:9–10)—labial tentacle (*q. v.*).

*Capsule* (Weill, 1934:21, 27–30)—hollow case of nematocyst.

*Cerinula* (Beneden, 1897:147; 1923:19)—larval stage with at least three couples of mesenteries.

*Ciliated tract* (Hertwig and Hertwig, 1879:557)—continuation of ciliated ectoderm and mesogloea from a furrow of the actinopharynx along one side of a mesenterial filament.

*Ciliated tract region* (Carlgren, 1912a:59–60)—trineme (*q. v.*).

*Cloison* (Fisher, 1887:383; Faurot, 1895:50)—mesentery (*q. v.*).

*Cloison prequatroseptale* (Beneden, 1897:24)—protomesentery (*q. v.*).

*Cloison primitive* (Beneden, 1897:23)—one of second couple of protomesenteries.

*Cloison quatroseptale* (Beneden, 1897:24)—metamesentery (*q. v.*).

*Cnida* (Gosse, 1858:125; 1860:xxii, xxix–xxxiv, 269; Weill, 1934:330)—nematocyst *sensu* Haime (*q. v.*).

*Cnida cochleata* (Gosse, 1858:126–127; 1860:xxxiii–xxxiv; Bedot, 1896:534; Weill, 1930:149)—spirocyst (*q. v.*).

*Cnida glomifera* (Gosse, 1858:126; 1860:xxxii–xxxiii; Weill, 1934:89–90) — nematocyst with nearly oval capsule containing long, isodiametric, loosely coiled tube (not in present use).

*Cnidoglandular tract* (Hertwig and Hertwig, 1879:557; Carlgren, 1949:8)—continuation



- of ciliated ectoderm from a ridge of the actinopharynx along the length of a mesenterial filament.
- Cnidoglandular tract* (Carlgren, 1912a:59-66)—plectocraspedon (*q.v.*).
- Cnidom* (Weill, 1926:1245; 1934:351)—nematocyst complement of coelenterate at any given moment of its existence.
- Cnidoneme* (Beneden, 1923:154)—acontoid (*q.v.*).
- Cnidorage* (Beneden, 1897:32; Carlgren, 1912a:72-73)—rounded projection of mesentery containing numerous nematocysts.
- Coelenteron* (Beneden, 1897:14)—main cavity of the animal.
- Column* (Gosse, 1860:2, 268; Beneden, 1897:9)—body cylinder below oral disc and tentacles.
- Column length*—internal distance from aboral end of actinopharynx to aboral pole.
- Commissural plane* (Faurot, 1895:50, 59)—directive plane.
- Continuous mesentery* (Heider, 1879:216-217; McMurrich, 1890:137)—mesentery reaching the aboral pore, especially applicable to a second protomesentery.
- Cordon pelotonné* (Haime, 1854:374)—mesenterial filament (*q.v.*).
- Couple of mesenteries* (Faurot, 1895:103; Beneden, 1897:20-21; Carlgren, 1906:66)—two corresponding mesenteries on opposite sides of directive plane.
- Craspedum* (Gosse, 1858:125; 1860:xxiii-xxiv, 5; Bourne, 1919:54-55; Torelli, 1960:374)—mesenterial filament (*q.v.*).
- Craspedion* (Carlgren, 1912a:60-68; Torelli, 1960:375-376)—telocraspedon (*q.v.*).
- Craspedoneme* (McMurrich, 1910:19-22)—threadlike or flattened, sometimes branched, process of the mesogloea and entoderm of mesentery over which pass ascending and descending limbs of mesenterial filament.
- Crown of tentacles* (Haime, 1854:350, 363; Faurot, 1895:218, 236-240)—all cycles of tentacles grouped around mouth or all cycles near edge of oral disc.
- Cycle of mesenteries* (Carlgren, 1912a:51)—order of mesenteries (*q.v.*).
- Cycle of tentacles* (Haime, 1854:365-367; Heider, 1879:213; Faurot, 1891:70-71)—ring of tentacles all equidistant from mouth or from margin of oral disc.
- d superscript* (Beneden, 1897:10-11)—droit, i.e. right with reference to the directive plane at the siphonoglyph.
- d superscript* (Beneden, 1923:23)—directive.
- D* (Beneden, 1897:20)—cloison directrice, i.e. directive mesentery (*q.v.*).
- Deuterocneme* (McMurrich, 1910:6-10)—metamesentery (*q.v.*).
- Directive chamber* (Carlgren, 1900:27; 1906:66)—Intermesenterial chamber between two directive mesenteries.
- Directive mesentery* (Hertwig and Hertwig, 1879:538, 572)—one of couple of mesenteries closest to directive plane at siphonoglyph.
- Directive plane* (Carlgren, 1906:66)—plane symmetrically bisecting the animal, running through siphonoglyph and point diametrically opposite as seen in cross-section.
- Directive tentacle* (Carlgren, 1900:25, 1906:66)—tentacle opening into directive chamber.
- dm.* (Carlgren, 1924a:169)—directive mesentery (*q.v.*).
- Dorsal*—opposite to ventral (*q.v.*).
- dt.* (Carlgren, 1924a:169)—directive tentacle (*q.v.*).
- Ecthoraeum* (Gosse, 1858:126; 1860:xxxi-xxxv, 269)—tube of nematocyst (*q.v.*).
- Enteroid* (Lacaze-Duthiers, 1873:302; Faurot, 1895:50-51, 234-235)—mesenterial filament (*q.v.*).
- Enterostome* (Beneden, 1897:14)—opening from cavity of actinopharynx into coelenteron.
- Filamentchen region* (Carlgren, 1912b:365)—telocraspedon (*q.v.*).
- Filamentseptum* (Heider, 1879:216; Carlgren, 1912a:51)—sterile mesentery (not in present use) (cf. Genitalseptum).
- Fils mésentériques* (Beneden, 1897:33)—craspedoneme (*q.v.*).
- g superscript* (Beneden, 1897:10-11)—gauche, i.e. left with reference to directive plane at siphonoglyph.
- Genitalseptum* (Heider, 1879:216; Hertwig and Hertwig, 1879:580-581)—fertile mesentery not reaching to aboral pore (cf. Filamentseptum).

- Grenzstreifen* (Carlgren, 1924b:347)—mesenteret (*q.v.*).
- Hampe* (Faurot, 1895:50)—main portion of mesentery excluding mesenterial filament.
- Hampe* (Weill, 1934:26)—shaft of nematocyst (*q.v.*).
- Hemisulcus* (Beneden, 1897:37–38; Carlgren, 1912a:50, 63)—continuation of half hypsulcus along edge of a directive mesentery.
- Holotrich* (Weill, 1930:145; 1934:37–38, 49–50, 64, 624–626; Cuttress, 1955:134–137)—basophilic nematocyst with an isodiametric, open-ended, tube armed along its entire length.
- Hoplotelic terminal tube* (Weill, 1930:147; 1934:38)—terminal tube bearing spines.
- Hyposulcus* (Beneden, 1897:15, 37–38; Carlgren, 1912a:50, 63)—grooved structure connecting the directive mesenteries, continuation of the siphonoglyph below the border of the actinopharynx.
- Intermesenterial chamber* (Faurot, 1895:228)—portion of coelenteron between two adjacent mesenteries.
- Isorbize* (Weill, 1930:145; 1934:37, 49, 624)—nematocyst with isodiametric tube open at tip.
- l* (Beneden, 1923:23)—loge de multiplication, i.e. multiplication chamber.
- L* (Beneden, 1897:10)—loge, i.e. intermesenterial chamber, other than directive chamber.
- L* (Beneden, 1923:23)—loge directrice, i.e. directive chamber.
- L with superscript* (Beneden, 1923:23)—loge other than directive chamber.
- Labial tentacle* (Haime, 1854:368–369)—tentacle of one of cycles surrounding mouth (cf. marginal tentacle).
- Lame* (Haime, 1854:371, 374)—mesentery (*q.v.*).
- Loge* (Haime, 1854:371)—intermesenterial chamber (*q.v.*).
- m* (McMurrich, 1910:14–15)—shorter macrocneme, i.e. macroseptum, of metamesenterial quartette.
- m* (Beneden, 1897:113)—multiplication chamber (*q.v.*).
- M* (McMurrich, 1910:14–15)—longer macrocneme, i.e. macroseptum, of metamesenterial quartette.
- M* (Beneden, 1897:10)—loge directrice, i.e. directive chamber (*q.v.*).
- Macrobasic mastigophore* (Weill, 1934:38, 64–68; Cuttress, 1955:133–134)—mastigophore in which shaft is more than three times capsule length.
- Macrobimesenterium* (Carlgren, 1912a:51)—macrobisepthum (*q.v.*).
- Macrobisepthum* (Beneden, 1897:23–24)—two longest mesenteries of a metamesenterial quartette.
- Macrocneme* (Stephenson, 1920:456)—mesentery of Actiniaria attached to actinopharynx with strong retractors, gonads, and filaments.
- Macrocneme* (McMurrich, 1910:14) macroseptum of Ceriantharia (*q.v.*).
- Macroseptum* (Faurot, 1891:68–69; 1895:233–234; Torelli, 1960:374)—one of two longest metamesenteries in a quartette.
- Marginal tentacle* (Haime, 1854:363–368)—tentacle of one of cycles near edge of oral disc (cf. labial tentacle).
- Mastigophore* (Weill, 1930:146; 1934:38, 58)—nematocyst with well-defined isodiametric shaft and terminal tube with open tip.
- Median plane* (Beneden, 1897:12)—directive plane (*q.v.*).
- Median streak* (Carlgren, 1912a:60–67)—spirocyst-glandular tract (*q.v.*).
- Median streak* (McMurrich, 1910:20–21)—central tract of trineme.
- Median tentacle* (Beneden, 1897:10)—directive tentacle (*q.v.*).
- Mesenterial length*—distance from aboral end of actinopharynx to aboral end of mesentery.
- Mesenterialfaden* (Hertwig and Hertwig, 1879:579–580)—craspedoneme (*q.v.*).
- Mesenterial filament* (Frey and Leuckart, 1847:12–18; Hertwig and Hertwig, 1879:556)—thickened rim running along free border of mesentery from end of actinopharynx aborally.
- Mesenteret* (Beneden, 1897:27; Carlgren, 1931:8)—projection of mesentery bearing the peloton.
- Mesentery* (Frey and Leuckart, 1847:11; Lacaze-Duthiers, 1873:301–302; Bourne, 1900:8–9)—longitudinal extension into coelenteron from body wall, attached to actino-

- pharynx and bearing thickened filament upon its free inner edge below actinopharynx.
- Mesogloea* (Bourne, 1887:303, 311–320; Torelli, 1952:154–156)—supporting layer between ectoderm and endoderm.
- Metacneme* (Duerden, 1900:47, 1902:388–397)—metamesentery (*q.v.*).
- Metamesentery* (Carlgren, 1912a:50–51, 59; 1912b:361)—any mesentery other than protomesenteries.
- Metasome* (Beneden, 1923:21–22)—central portion of body excluding prosome and telomere (*q.v.*). (by analogy to *Amphioxus*).
- Microbasic mastigophore* (Weill, 1934:38, 58–64, 624–626)—mastigophore in which shaft is at most three times capsule length.
- Microbimesenterium* (Carlgren, 1912a:51)—microbiseptum (*q.v.*).
- Microbiseptum* (Beneden, 1897:23–24)—two shorter mesenteries of metamesenterial quartette.
- Microseptum* (Faurot, 1891:68–69; 1895:233–234; Torelli, 1960:374)—one of two shortest metamesenteries in quartette.
- Mononeme* (Beneden, 1923:79–80)—aboral monofilar region of mesenterial filament.
- Mouth* (Rapp, 1829:654; Haime, 1854:350, 372)—opening from exterior to cavity of actinopharynx.
- Mucocraspedoneme* (Carlgren, 1912a:71)—acntioid (*q.v.*).
- Multiplication chamber* (Vogt, 1888:24)—intermesenterial chamber opposite directive chamber, in which new mesenterial couples are formed.
- Mundscheibe* (Hertwig and Hertwig, 1879:471; Heider, 1879:212)—oral disc (*q.v.*).
- Nematocyst* (Haime, 1854:354–357, 365; Bedot, 1886:51–52; Cuttress, 1955:124–126)—capsule containing an expellable coiled tube.
- Nematocyst* (Bedot, 1889:607–608; 1896:535–536; Weill, 1934:330)—nematocyst *sensu* Haime excluding spirocysts.
- Odd tentacle* (Agassiz, 1863:527; Fischer, 1889:24)—directive tentacle (*q.v.*).
- Oesophagus* (Haacke, 1879:276, 293; Jourdan, 1879:103, 108–109)—actinopharynx (*q.v.*).
- Oral disc* (Faurot, 1895:47–48, 218)—disc at one end of animal bearing mouth and tentacles.
- Order of mesenteries* (Carlgren, 1912b:375–376, 386; Torelli, 1960:374)—all metamesenteries of same relative lengths in their respective quartettes.
- Orthocraspedon* (Bourne, 1919:55–57)—trineme (*q.v.*).
- p. superscript* (Beneden, 1923:23)—belonging to third somatome of prosome (*q.v.*).
- P* (Carlgren, 1912:8)—protomesentery (*q.v.*).
- Peloton* (Faurot, 1895:235–236; Beneden, 1897:27, 46; 1923:51–52, 79)—highly convoluted section of mononeme.
- Penicillus* (Stephenson, 1929:178–179; Weill, 1934:91–92)—nematocyst containing short, stout, armed tube (not in present use).
- Peristome* (Vogt, 1888:29)—portion of oral disc between tentacle crowns.
- Plectocraspedon* (Bourne, 1919:55–57)—portion of mononeme indistinctly delimited by abundance of large, thick-walled nematocysts and large coarsely-granular gland cells, usually anterior to telocraspedon.
- p-mastigophore* (Carlgren, 1940:3–4; Cuttress, 1955:129–131, 133–134; Hand, 1961:189–190, 193)—mastigophore in which abrupt reduction of shaft to terminal tube allows funnel-shaped invagination of axial body.
- Protocneme* (Duerden, 1900:47; McMurrich, 1910:6–10)—protomesentery (*q.v.*).
- Protomesentery* (Carlgren, 1912a:50–51, 59, 1912b:361)—one of mesenteries arising in first embryological stage (presently considered to be one of the first three mesenteries on either side of directive plane at siphonoglyph).
- Prosome* (Beneden, 1923:21)—anterior portion of body including three cycles of protomesenteries and associated tentacles, intermesenterial chambers adjoining and portions of columnar wall, peristome and actinopharynx (by analogy to *Amphioxus*).
- Quartette of metamesenteries* (Faurot, 1891:67–68; 1892:238; 1895:231–234)—any group of four mesenteries in a series as counted from protomesenteries, each group showing similar pattern of relative mesenterial lengths.

- Quatromere* (Beneden, 1924:43)—four successive somatomes (q.v.).
- S.* (Beneden, 1897:20)—cloison, i.e. mesentery, other than directive mesenteries.
- S with superscript* (Beneden, 1923:25)—sarco-septum, i.e. mesentery.
- Sarcoseptum* (Haacke, 1879:277, 293)—mesentery (q.v.).
- Sarcosepte antipathoide* (Beneden, 1923:18)—protomesentery (q.v.).
- Sarcosepte cerianthoide* (Beneden, 1923:19)—metamesentery (q.v.).
- Schlundrinne* (Hertwig and Hertwig, 1879: 513, 572)—siphonoglyph (q.v.).
- Septum* (Gosse, 1860:xiii-xiv, 5, 268)—mesentery (q.v.).
- Shaft* (Carlgren, 1940:3)—thickened basal part of tube, of some nematocysts.
- Siphonoglyph* (Hickson, 1883:693-694; McMurrich, 1890:131, 136)—smooth ciliated groove of actinopharynx.
- Somatomere* (Beneden, 1923:21-22)—“segment” of body including a couple of mesenteries, the intermesenterial chambers ‘anterior’ to them, and the associated tentacles and adjoining portions of columnar wall, peristome and actinopharynx (by analogy to *Amphioxus*).
- Spiral cnida* (Gosse, 1858:126-127; 1860: xxxiii-xxxiv; Weill, 1934:326)—spirocyst (q.v.).
- Spirocyst* (Bedot, 1889:607-608; 1896:534-536; Weill, 1934:325-342, 624; Cuttress, 1955:124-126, 136)—capsule containing an acidophilic, very regularly spiralled, tube of uniform diameter which irregularly everts (cf. *Holotrich*).
- Spirocyst-glandular tract* (Carlgren, 1912a:60-67)—telocraspedon and histologically similar medial tract of trineme.
- Spirula* (Stephenson, 1929:179; Weill, 1934: 91-92)—nematocyst containing long slender tube with enlarged or armed basal portion (not in present use).
- Stomatodaenum* (McMurrich, 1890:136)—actinopharynx (q.v.).
- Stomodaenum* (Bourne, 1900:7, 51)—actinopharynx (q.v.).
- Sulculus* (Haddon, 1889:300)—siphonoglyph other than the sulcus of Actiniaria (q.v.).
- Sulculus* (Carlgren, 1912a:55-56)—siphonoglyph of Ceriantharia if considered homologous to sulculus of Actiniaria (q.v.).
- Sulcus* (Haddon, 1889:300)—ventral siphonoglyph of Actinaria, i.e. that one homologous to single siphonoglyph of *Peachia*.
- Sulcus* (Kingsley, 1904:347-351; Torelli, 1960: 383) siphonoglyph of Ceriantharia if considered homologous to sulcus of Actiniaria (q.v.).
- t* (Beneden, 1897:10-11)—labial tentacle other than directive tentacle.
- t* (Beneden, 1923:23)—labial directive tentacle (q.v.).
- t with superscript* (Beneden, 1923:23)—labial tentacle other than directive tentacle.
- T* (Beneden, 1897:10-11)—marginal tentacle other than directive tentacle.
- T* (Beneden, 1923:23)—median marginal tentacle, i.e. marginal directive tentacle.
- T. with superscript* (Beneden, 1923:23)—marginal tentacle other than directive tentacle.
- T.M.* (Beneden, 1897:10-11)—median marginal tentacle, i.e. marginal directive tentacle.
- Telocneme* (McMurrich, 1910:11-13)—continuous mesentery (q.v.).
- Telocraspedon* (Bourne, 1919:55-57)—portion of mononeme indistinctly delimited by abundance of spirocysts and eosinophilous mucus gland cells, usually posterior to plectocraspedon.
- Telomere* (Beneden, 1923:22)—“segment” of body including multiplication chamber (by analogy to *Amphioxus*).
- Terminal tube* (Weill, 1934:26, 37)—thin distal part of tube, in some nematocysts.
- Thread* (Gosse, 1858:126; 1860:xxix-xxxiv)—tube of nematocyst (q.v.).
- Thread* (Carlgren, 1940:3)—terminal tube of nematocyst or entire tube of thickened basal portion is absent.
- Trineme* (Beneden, 1923:79-80)—adoral trifilar region of mesenterial filament.
- Tube* (Weill, 1934:21-22, 36-38)—eversible hollow structure coiled within capsule of nematocyst.

*Ventral* (Kolliker, 1870–1872)—end of directive plane on which single siphonoglyph of pennatulids is placed (by convention).

*Ventral* (Beneden, 1897:12) — aboral portion of column of Ceriantharia (by analogy with the orientation of *Amphioxus*).

*Ventral* (Haacke, 1879:294; Carlgren, 1893: 242–246; 1912a:54–58)—end of directive plane opposite single siphonoglyph of Ceriantharia if siphonoglyph is not considered homologous to that of the pennatulids.

*Ventral* (Herrwig and Hertwig, 1879:572; Faurot, 1895:62, 228, 250; McMurrich, 1910:9; Torelli, 1960:383)—end of directive plane on which single siphonoglyph of the Ceriantharia is placed if it is considered homologous to siphonoglyph of pennatulids.

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# The Geographical Affinities of the South Pacific Island Fern Floras

G. BROWNLIE<sup>1</sup>

**ABSTRACT:** The theory is proposed that the fern floras of the South Pacific, while being predominantly recently Malaysian in origin, consist also of two older elements, one being relics only of an ancient world-wide flora, the other an earlier Malaysian invasion confined now to the older and larger islands only. A fourth minor element is a recently evolved southern or subantarctic group.

MUCH HAS BEEN WRITTEN in texts on plant geography on the importance of Pacific island floras, and many papers have discussed the elements present in these floras, but these have relied largely on analyses of the phanerogams only. It is felt that the other groups of plants may yield as much information of interest, and an attempt is made here to examine the fern floras of the South Pacific from this point of view. Most of these floras are fairly well-known now, although written information for the New Hebrides is scattered, and material for the Solomons is very incomplete.

The most outstanding immediate impression is the gradual reduction in number of species from the Solomon Islands eastwards and southwards. Most of the smaller islands of course do not possess the range of habitats suitable for the establishment or development of a very diverse flora, but this general principle still applies to relatively large high islands. Copeland (1929) admits 230 species for Fiji, Christensen (1943) lists 213 for Samoa, Copeland (1932) gives 150 for the Society Islands, while New Zealand also possesses 150 species. By contrast with this, at least 300 species are known from New Caledonia with probably a much greater number in the islands to the north.

Elevation also plays a vital role in the diversity of fern floras, islands with sufficiently high mountains to develop a definite mist zone

having a very much greater number of species than low-lying islands in the same area. Wet mountain forests throughout the tropics are always the sites of the most prolific display of specific and generic variety. In Borneo, of the total of some 700 species, approximately 400 have been recorded from the single large massif of Mt. Kinabalu. An example of the difference that this factor makes is shown by a comparison of the flora of New Caledonia with that of the neighbouring low-lying Loyalty Islands. The latter possess only about 30 species—all widespread ferns or local variants of widespread species, and none of the typically New Caledonian groups are represented. This flora, which may almost be called a tropical weed fern flora, is characteristic of all low Pacific islands, the same species occurring throughout. On atolls the number of species is further reduced, but all are members of this same group.

The majority of fern genera are so widespread geographically that any attempt to distinguish relationships, evolution, and directions of distribution using this rank as a criterion becomes meaningless. This does not exclude the possibility that experimental work within any genus will not give hints as to the evolution of the genus, and of relationships both within the genus and to other genera, but most investigations of this type would need to be carried out on such a vast scale that they would occupy more than one researcher's lifetime. Consequently the pattern of specific distributions has been found the most productive in

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giving any impression of the relationships existing among various Pacific island floras.

The only locally endemic genera in the area under discussion are *Loxsonia* in northern New Zealand and *Stromatopteris*, a monotypic member of the Gleicheniaceae confined to the open serpentine region in the south of New Caledonia. It is interesting that these occur in the two island groups with the longest geological history.

#### SAMOA AND THE SOCIETY ISLANDS

Similarities are most striking when the floras of Fiji, Samoa, and the Society Islands are compared with one another. Of the total of approximately 200 species in Samoa only 32, or 16%, are endemic, and all of these are species closely related to other local species or to ones found in Fiji. A critical comparison of the endemic species of the various Pacific islands is required because in the past there has been a marked tendency to give specific rank to any local form which varies at all from the described type, often on the basis of a single collection. This is most apparent in large and difficult genera such as *Asplenium* and *Cyclosorus*. The eight Samoan species with peculiar distribution and found nowhere else in Polynesia, as noted by Christensen (1943), are all open to misinterpretation, each apparently being based on single, possibly aberrant, individuals. Of the remaining non-endemic species, practically all are found in Fiji.

The picture presented for Samoa is repeated with minor variations in the Society Islands. Here there are approximately 150 species of ferns of which 30% are regarded as endemic. This appears to be a somewhat high figure when it is noted that Tahiti is geologically younger than Fiji with only 20% of endemics, but it may be explained on the basis of the greater elevation of the former and its greater isolation. A more likely explanation when comparing the percentage of endemics in these islands may lie in the relative propensities of the various authors to recognize local variants as true species. Again all of the Society Islands' endemics are close to other local species or to species found elsewhere in Polynesia, and Copeland (1932) admits that one, *Polypodium*

*maximum* (Brack.) Hook., may be an interspecific hybrid. This aspect of hybridism which is known to occur in some fern groups in New Zealand may explain several of the rare species which appear in so many Pacific island lists on the basis of a single collection.

The remaining high island groups of southern Polynesia, the Cook Islands, Tonga, the Marquesas, and the Australs, have fern floras which are only extensions of the three major areas, Fiji, Samoa, and the Society Islands.

#### FIJI

Fiji represents possibly the immediate source of the fern flora of central and eastern Polynesia. Geologically it is older than these other islands and its flora is larger. However only just over 20% of this large number are endemic, and again all of these are closely related to other local species or to species on other Pacific islands, including this time the New Hebrides. Approximately 60% of the total species known in Fiji occur in these islands to the west, many extending as far as New Guinea and Indonesia. In addition to these common species, many pairs of closely related species occur in the southern islands of the New Hebrides such as *Aneityum* and Fiji. Examples of these pairs of species are *Humata botrychioides* Brack. in Fiji and *Humata multifida* (Baker) Carr. ex Brownlie in the New Hebrides, and *Orthiopteris ferulacea* (Moore) Copeland of Fiji and *Orthiopteris kingii* (Bedd.) Holtt. of the New Hebrides and farther west.

The whole effect then of the fern floras of the islands from the New Hebrides eastwards into the Pacific is that of a Malaysian group becoming gradually depleted the farther east it is traced, with probable secondary centres of diversification in the New Hebrides themselves and in Fiji.

#### NEW CALEDONIA

Perhaps the most interesting island from a phytogeographical viewpoint is New Caledonia. This has been realised for many years in the case of the phanerogamic flora of that island, to judge by the number of publications

on and references to the subject. An analysis of the fern flora reveals a corresponding diversity which contrasts markedly with the rather uniform Malaysian relationship of the floras of the other tropical Pacific islands. Of the approximately 300 species 127, or nearly 42%, are endemic. This is a very high proportion of plants belonging to such an old group to be confined to one island, and can only be explained on the basis of the presence of a land mass somewhere in the region for a much longer period than is the case for the other island groups discussed. Fournier (1874) postulated a greater Melanesia somewhere in this area as a source of much of the New Caledonia pteridophyte flora.

In addition to this the appearance of the flora is not so overwhelmingly that of the wet Malaysian type found in the other islands. At least a quarter of the endemic species are truly distinctive, and not merely local variant species of genera such as *Asplenium* which appear to have undergone recent evolution and speciation. The presence of several species in ancient groups like the Schizaeaceae and the Gleicheniaceae suggests relic forms from a much older period of diversification. Much interest also lies in the large number of endemic species belonging to the Lindsaeoid group of ferns. Cytological investigations on this group suggest that it possibly consists of two sections—one a fairly ancient group diversified from one another as to chromosome numbers ( $n = 34, 42, 47$ ), and a fairly uniform group with a chromosome complement based on  $n = 50$  which is typically Malaysian in distribution. It appears likely that the non-endemic species in New Caledonia belong to the latter, while the large number of taxonomically difficult local species are older forms which may not be even closely related to the widespread ones. It is also significant that most endemics of all the old groups are confined to the poorer soils of the island and to mountain ridges, while the more aggressive widespread recent Malaysian forms occupy the rain forests and the better soils.

A third element enters to a minor degree into the New Caledonian flora. This is the small group of species which are directly re-

lated to those of eastern Australia, although they are possibly indirectly also Malaysian. The various species of *Cheilanthes* would fall into this category. Some of these species occur in Malaysia but not in the humid equatorial region north of New Caledonia. Others are specifically Australian derivatives of this group.

#### NEW ZEALAND

The final major region in the South Pacific is New Zealand. Here the number of species is considerably less than that of New Caledonia, Fiji, or Samoa, being approximately the same as that for the most easterly sizeable group, the Society Islands. However, a comparison of the two fern floras shows major differences. Whereas the Society Islands possess no endemic genera, New Zealand has the local *Loxsonia* and an elaboration of ancient groups only surpassed in New Caledonia. A further similarity with New Caledonia is shown by the fact that the three local species of *Lindsaea* (*L. linearis* Sw., *L. trichomanoides* Dry., and *L. viridis* Col.) are cytologically distinct from one another. It seems possible that on the basis of their chromosome contents the rather isolated genera *Loxsonia* and *Leptolepia* are more nearly on the same evolutionary level, and possibly more nearly related to this old section in the Lindsaeoid group of ferns than to any other (Brownlie 1961, and unpublished).

At least one third of the New Zealand species are endemic, but here the relationships of these endemics are not with the tropical Malaysian element of the Pacific but most frequently with closely related species in eastern Australia. This relationship is so close that somewhat more than 50% of the total New Zealand fern flora is found also in the southeastern part of Australia and Tasmania (Brownlie, 1962*b*).

#### THE 'ANTARCTIC' ELEMENT

A theory which has been made much of by Copeland (1939 and 1947) is the antarctic origin of much of the world's modern fern flora. This theory was based on his belief that within different genera those showing the most primitive morphological characters were those species occurring in southern lands. The evi-

dence for this is inconclusive and may be interpreted in other ways. There is, however, within the Pacific fern floras a distinctive southern element which may in part be of recent origin. The genus *Polystichum* is a member of this group and is best developed in New Zealand and eastern Australia, but it extends northward into the Society Islands. One species is completely circum-polar and related or similar species occur in temperate South America.

*Asplenium obtusatum* Forst., or species very like it in both form and habitat, also occurs widely around the subantarctic extending north into eastern Polynesia. The present range in the colder parts of the Southern Hemisphere and the extreme polymorphism of this group suggests a recent origin. To this southern group probably also belong several New Zealand species of *Blechnum*, including those of the *B. procerum* complex, and some species of *Grammitis*. Only one other species, *Hymenophyllum ferrugineum* Colla, is common only to temperate South America and New Zealand. This is a much slighter relationship than could be expected if Copeland's theory of an antarctic origin were acceptable, even more so when the much-discussed similarities between the phanerogams are compared with it.

#### ISOLATED ISLANDS

It may be of interest to examine the floras of a number of South Pacific islands which are sufficiently isolated not to belong to any group. Pitcairn Island at the extremity of eastern Polynesia has a fern flora of only 19 species, all of which are similar to or only doubtfully distinct from those of the Society and Austral Islands (Brownlie, 1962a). This appears to be a recent flora with little or no time for local differentiation, and with none of the distinctive species of the nearest groups included. Presumably these species which have succeeded in colonising the most south-easterly extension of Polynesia are among the most successful in dispersal of the Malayan-Polynesian ferns.

Rotuma Island, an isolated volcanic cone northwest of Fiji, has a fern flora consisting of 26 species (St. John, 1954). Again, most of the species are those of wide distribution in

the tropical Pacific with one endemic, *Clycosorus rotumaensis* St. John, closely related to Fijian species, and one, *Tectaria dimorpha* St. John, whose relationships appear doubtful. This latter belongs to a group much in need of complete revision in the Malaysian-Pacific area. The most obvious similarities of the whole flora are with Fiji and the New Hebrides.

Norfolk Island, although closer to New Zealand and with many ferns in common with that country, also has several species more obviously belonging to eastern Australia. Of the total of 38 species noted by Laing (1915) only three or four are endemic, the remainder being either widespread Pacific species which occur also in Australia, or definite Australian representatives. The almost complete Australian relationship of the flora suggests long range wind dispersal as the most likely mode of arrival.

Lord Howe Island, due to its greater altitude and consequent variety of habitat, has a somewhat larger flora than Norfolk Island (Oliver, 1917) but here again the relationship is predominantly with the Australian mainland. There is, however, a suggestion of a somewhat older group shown by the endemic elaboration of the Hymenophyllaceae, a character lacking in the other isolated islands mentioned. This speciation in the *Eu-Hymenophyllum* and *Meringium* sections of the genus *Hymenophyllum* is otherwise confined to the older or larger areas, New Zealand, New Caledonia, eastern Australia, and to a minor extent Fiji. Another interesting fact is the doubtful distinction between *Asplenium pteridoides* Baker of Lord Howe and *A. polyphyleticum* Compton of New Caledonia. It seems that the fern flora of Lord Howe is not merely one with an immediate relationship to the nearest source of supply, as is the case with Pitcairn, Rotuma, and Norfolk.

#### DISCUSSION

The outstanding impression of the whole fern flora of the South Pacific is that it is an extension eastwards of the one found in the Malaysian area, with a gradual reduction in numbers towards the east. This is most obvious if the islands to the south of the New Hebrides are omitted. When New Caledonia and

New Zealand are included the situation appears somewhat more complex. The bulk of the flora of New Caledonia is related to that of northern islands but a not inconsiderable portion is characteristic either of that island only, or of New Zealand, eastern Australia, and New Caledonia as a unit.

It is suggested that the fern flora of this region consists of four groups:

1. An ancient group of primitive families of an old world-wide flora with a large number of its southern relics persisting in New Caledonia and New Zealand. This would include the representatives of the Osumdaceae, Schizaeaceae, and Gleicheniaceae.

2. An intermediate period flora whose relationships are somewhat obscure but which may represent an earlier Malaysian invasion of the region. Again this persists only in New Caledonia, New Zealand, and eastern Australia, and includes the Lindsaeoid endemics of New Caledonia, *Loxsoma*, *Dicksonia*, *Leptolepia*, and at least the sections *Eu-Hymenophyllum* and *Meringium* of *Hymenophyllum*.

3. A recent Malaysian section forming the bulk of the flora, and found in all areas including eastern Australia and New Zealand (where it may have arrived indirectly by wind dispersal from Australia).

4. A recently evolved southern element most conspicuous in New Zealand and eastern Australia but extending into eastern Polynesia.

The possibility remains that many of the pan-tropical and other widespread Pacific species, such as those of *Nephrolepis*, may have been aided in their distributions by human migrations in the area.

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## Revision of the Genus *Pandanus* Stickman, Part 19

### Additional Malayan Species of *Pandanus*

HAROLD ST. JOHN<sup>1</sup>

MOST OF THE MALAYAN SPECIES of *Pandanus* have already been treated by the writer in parts 11, 14, and 15 of this revision. Here are presented descriptions of five of the remaining species.

*Pandanus elostigma* Martelli, Soc. Bot. Ital., Bul. n. s. 11(2):302-303, 1904; *Webbia* 4(1): 13, 1913; 4(2):t. 30, fig. 9, 1914; Ridley, Fl. Malay Penin. 5:79, 1925. (sect. *Acrostigma*).

Fig. 219

NOM. VERN.: "shidayen masing."

**DIAGNOSIS OF LECTOTYPE:** Apparently a low shrub, growing in clusters of as many as 20; leaves 1-2.24 m long, 18.5-22 mm wide, thick firm chartaceous, above dark bluish green, below bluish green, 1-ribbed, 2-pleated, the central furrow narrow, in section M-shaped, at midsection with 19-22 parallel secondary veins in each half, these prominent throughout, tertiary cross veins visible  $\frac{1}{3}$  way from the base and in outer half conspicuous, more or less transverse and forming short oblong meshes, the blade ligulate but in upper  $\frac{1}{6}$  gradually narrowing to a trigonous subulate apex about 5 cm long, 1.5-2 mm wide, the base unarmed, but beginning 13-16 cm up the margins with prickles 0.6-0.9 mm long, 3-5 mm apart, heavy subulate, ascending, pale; the midrib below with a few prickles beginning at 10.5 cm up and 1-1.7 mm long, 4-11 mm apart, conic subulate, reflexed; at midsection the margins with delicate prickles 0.4-0.5 mm long, 3-5 mm apart, subulate, closely appressed; the nearby midrib unarmed; on the subulate apex the margins with subulate tipped serrulations 0.3-0.4 mm long, 1-2 mm apart; the midrib below with similar serrulations 1.5-7 mm apart; syncarp 8-12.5 cm long, 5-7.5

cm in diameter, bluish green, solitary, terminal, subglobose; drupes 23-26 mm long, 5-6 mm wide and thick, fusiform, the body 11-13 mm long, oblanceoloid, fleshy but when dry the apex shrunk and much smaller than the flaring base of the pileus; pileus 1.5-2 mm high, smooth, the base discoid, firm, but when dried flaring and undulate; style 9-10 mm long, thick subulate, mostly proximally curved, the lower half with 4-6 sharp angles but the intervals flat or furrowed, the upper half terete; stigma 6-7 mm long, linear, distal, brown, papillose, running to the tip; endocarp centering in lower  $\frac{2}{7}$ , cuneate the walls 0.1 mm thick, pale brown, except near the apex, formed principally of the heavy, longitudinal, marginal fibers, these connected by a thin tissue; apical mesocarp 5 mm long, ellipsoid from a truncate base, containing only the white membranes of an aerenchyma; basal mesocarp fleshy and fibrous.

**LECTOTYPE:** Malay Peninsula, Perak, Larut, in large clusters on rocky soil, 300 to 800 ft alt, Sept. 1884, *Dr. King's Collector* 6,559 (CAL)! Isotype (SING)!

**SPECIMENS EXAMINED:** Malaya, Perak, Larut, open ground, 300 ft alt 1883, *Dr. King's Collector* 3,758 (CAL, SING) This is also in (FI) but by error as 3,755. Malacca, Gaong dalam Ayer Panas, Oct. 1893, *J. S. Goodenough* 1,535 (CAL).

**DISCUSSION:** As Martelli originally described this species from two collections, one is here chosen as lectotype.

The illustrations of two drupes published by Martelli in 1914 show well the remarkable flaring base of the pileus. Our illustration, Figure 219 *b, e*, shows a dried drupe similar to his, but our Figure 219 *a, d*, shows one after boiling. In this one the lower pileus flange has rounded out

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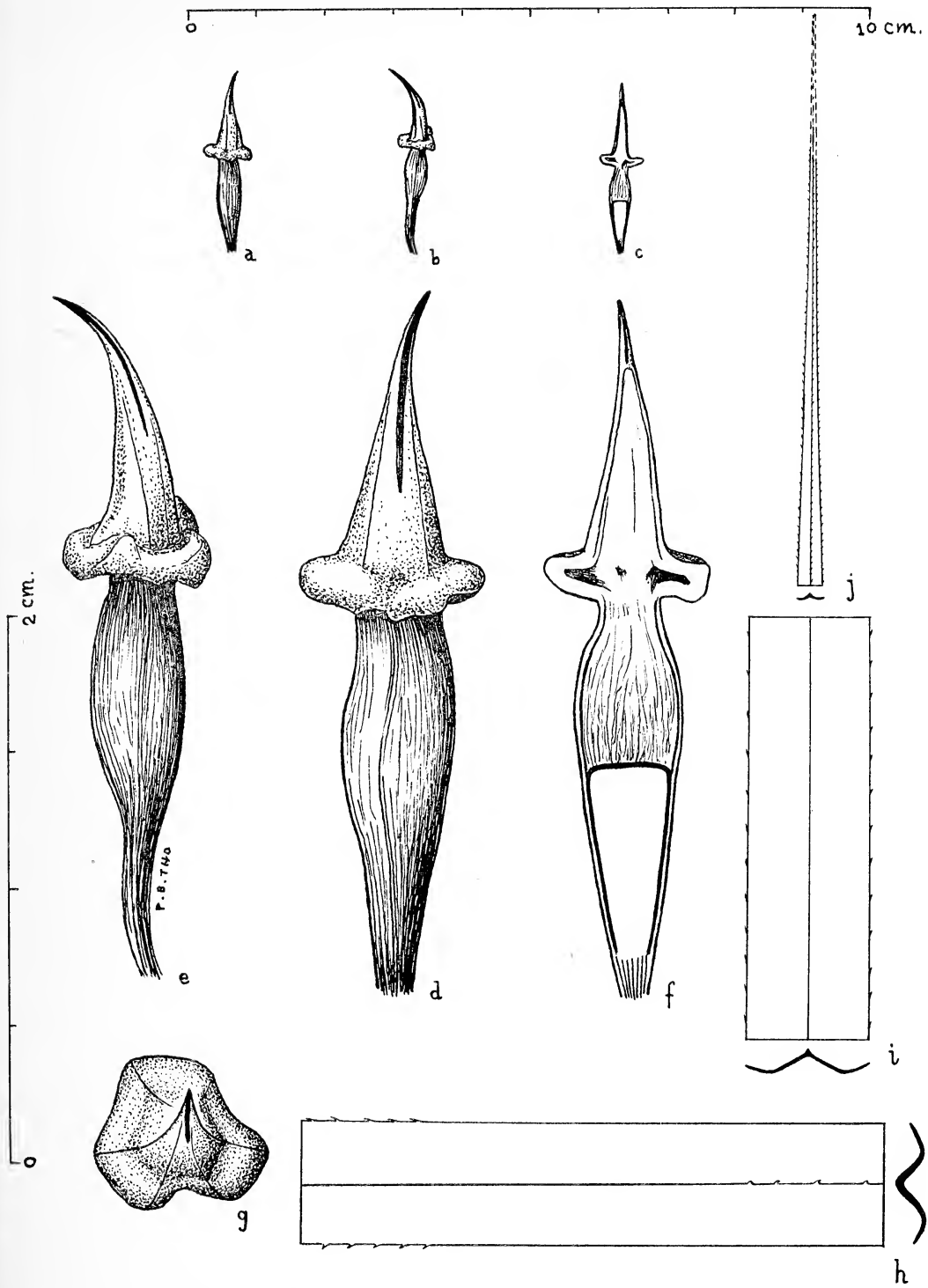
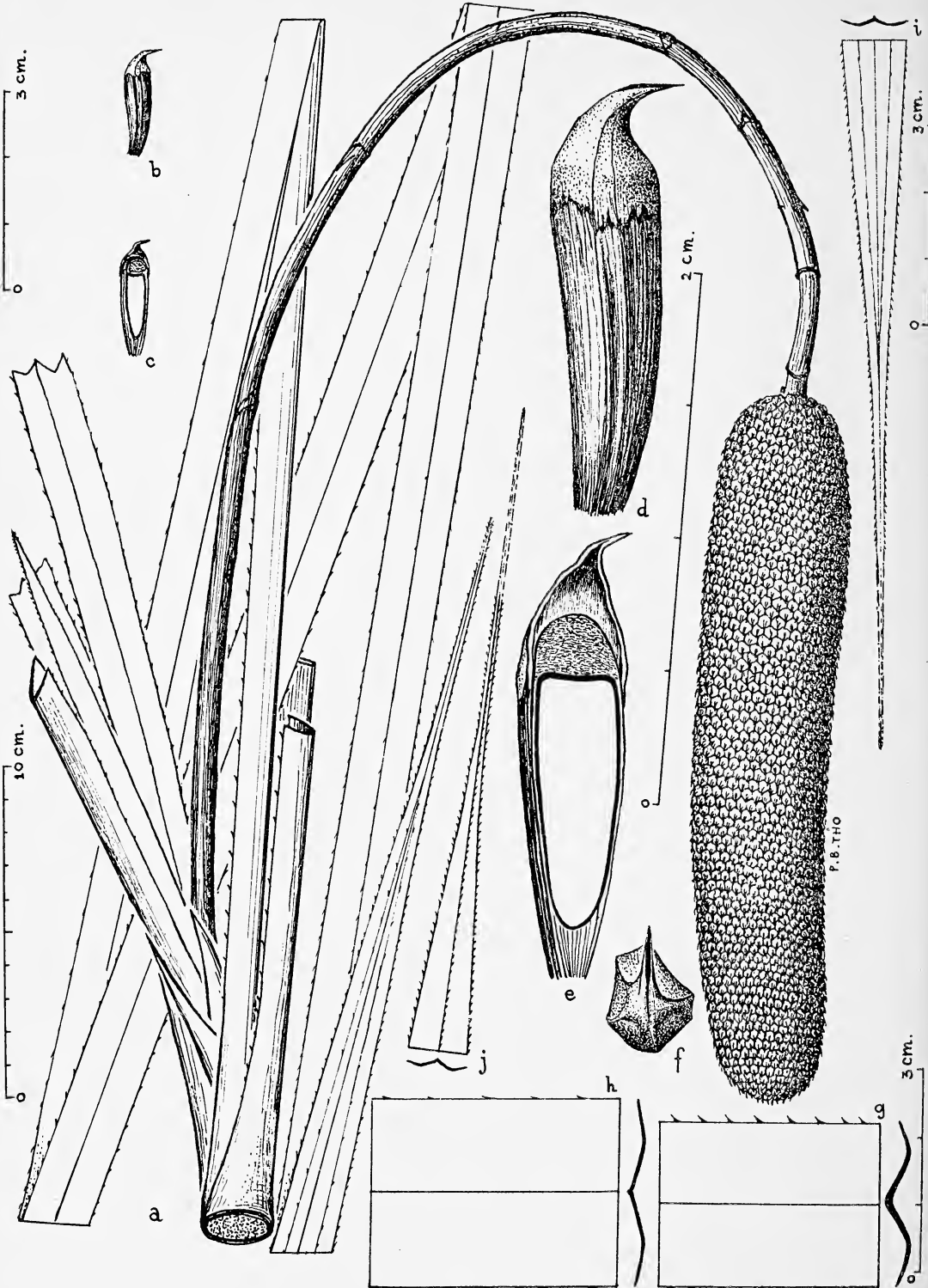


FIG. 219. *Pandanus elostigma* Martelli, from lectotype, Larut, Dr. King's Collector 6,559 (SING). *a*, *b*, drupe, lateral view,  $\times 1$ ; *c*, drupe, longitudinal median section,  $\times 1$ ; *d*, boiled drupe, lateral view,  $\times 4$ ; *e*, dried drupe, lateral view,  $\times 4$ ; *f*, drupe, longitudinal median section,  $\times 4$ ; *g*, drupe, apical view,  $\times 4$ ; *h*, leaf base, lower side,  $\times 1$ ; *i*, leaf middle, lower side,  $\times 1$ ; *j*, leaf apex, lower side,  $\times 1$ .





and reassumed a horizontal position and with the lower edge revolute. The outer surface of the pileus is hard, almost cartilaginous, but when dried it becomes irregularly wavy. When fresh the fleshy body must have been as wide as the base of the pileus. This species is unique and very distinct.

Martelli described the drupes as 15–17 mm long, but in his life-sized figure he showed them as 28–29 mm long. In the lectotype here described, they are 23–26 mm long. Martelli retained a portion of *Dr. King's Collector* 3,758 (erroneously as 3,755) with two parts of a leaf and 13 loose drupes. These are from 29–33 mm long. It would seem that the measurements given in his publication were erroneous.

*Pandanus recurvatus* sp. nov. (sect. *Acrostigma*).

*Fisquetia ornata* Gaud., Voy. La Bonite, Bot. t. 5, figs. 1, 8, 9, 1843, an invalid name which cannot be transferred.

*P. ornatus* Kurz (as (Gaud.) Kurz), Asiat. Soc. Bengal, Jour. 38(2):147, 1869, but not *P. ornatus* Hort. ex Bull. R. Hort. Soc., Jour. n. s. 1: misc. 1, 1866.

*P. ornatus* Solms-Laubach, Linnaea 42:11, 1878, published without a description; Ridley, Fl. Malay Penin. 5:80, 1925; Martelli, Webbia 4(1):26, 1913.

*P. ornatus* Kurz, forma *spicata* Martelli, Webbia 4(2):432, 1914.

Figs. 220–221

NOM. VERN.: "pandan beduri."

DIAGNOSIS HOLOTYPE: Frutex, foliis 1.68 m longis 2.9 cm latis firme chartaceis supra griseo-viridibus infra pallidis glaucisque supra midnervum U-sulcatis 2-plicatis in sectione mediali cum 27–31 nervis parallelis secundariis in quaque media infra ad apicem cum nervis tertiis transversis reticulis oblongis formantibus laminis ligulatis sed ad apicem in apice trigono subulato 4–7 cm longo diminuentibus basi inermi subcoriacea, marginibus ex 6–8 cm cum aculeis 1.5–2 mm longis 3–7 mm separa-

tis subulatis gracilibus adscendentibus pallidis, midnervo infra per mediam inferam inermi, in sectione mediali marginibus cum aculeis 0.5–1 mm longis 4–11 mm separatis subulatis adpresse adscendentibus, supra in tertia ultima plicis cum subulato-serrulis 0.3–0.5 mm longis 3–10 mm separatis, in apice marginibus et midnervo infra cum serrulis 0.3–0.5 mm longis eis marginalibus 1–2.5 mm separatis illis midnervi 2–4 mm separatis, infructescentia terminali cum syncarpio unico, pedunculo 22 cm longo 7 mm diametro 3-laterato bracteato recurvato, syncarpio 23.4 cm longo 4.2 cm diametro cylindrico cum drupis multitudinis, drupis 18 mm longis 3.4 mm latis et crassis oblongo-oblanceoloideis 4–6-angulosis apice subulato corpore 9–14 mm longo, pileo 3–4 mm alto obliquiter conico laevi plerumque subangulato, stylo 3.5–5 mm longo subulato rigido valde proxime arcuato, stigmate 2–4 mm longo lineari distali brunneo papilloso, endocarpio in parte  $\frac{1}{3}$  infera lateribus lateralibus 0.1 mm crassis stramineis, mesocarpio apicali meduloso, mesocarpio basali parvo fibroso et carnoso.

#### DESCRIPTION OF ALL SPECIMENS EXAMINED:

Shrub 2–5 m tall, dense, much branched, erect; stem gray, at apex 12–15 mm in diameter, "thorny above," with prop roots 6 mm in diameter; leaves 1.2–2 m long, 1.3–2.9 cm wide, firm chartaceous, grayish green above, pale and glaucous beneath, with a deep furrow above the midrib and 2 lateral pleats, in section M-shaped, the secondary parallel veins visible throughout and at midsection 27–31 in each half, towards the tip on the lower side with a few visible tertiary cross veins making elongate oblong meshes, the blade ligulate, but near the tip gradually tapering into a 4–7 cm subulate, trigonous, caudate tip, 0.5–0.9 mm wide, the base unarmed, firm, subcoriaceous, beginning 6–8 cm up the margins with prickles 1.5–2 mm long, 3–7 mm apart, subulate, diverging or ascending, pale; the midrib below for the lower half unarmed; at midsection the

FIG. 220. *Pandanus recurvatus* St. John, from holotype. *a*, fruiting branch, lateral view,  $\times 1$ ; *b*, drupe, lateral view,  $\times 1$ ; *c*, drupe, longitudinal median section,  $\times 1$ ; *d*, drupe, lateral view,  $\times 4$ ; *e*, drupe, longitudinal median section,  $\times 4$ ; *f*, drupe, apical view,  $\times 4$ ; *g*, leaf base, lower side,  $\times 1$ ; *h*, leaf middle, lower side,  $\times 1$ ; *i*, leaf apex, upper side,  $\times 1$ ; *j*, leaf apex, lower side,  $\times 1$ .

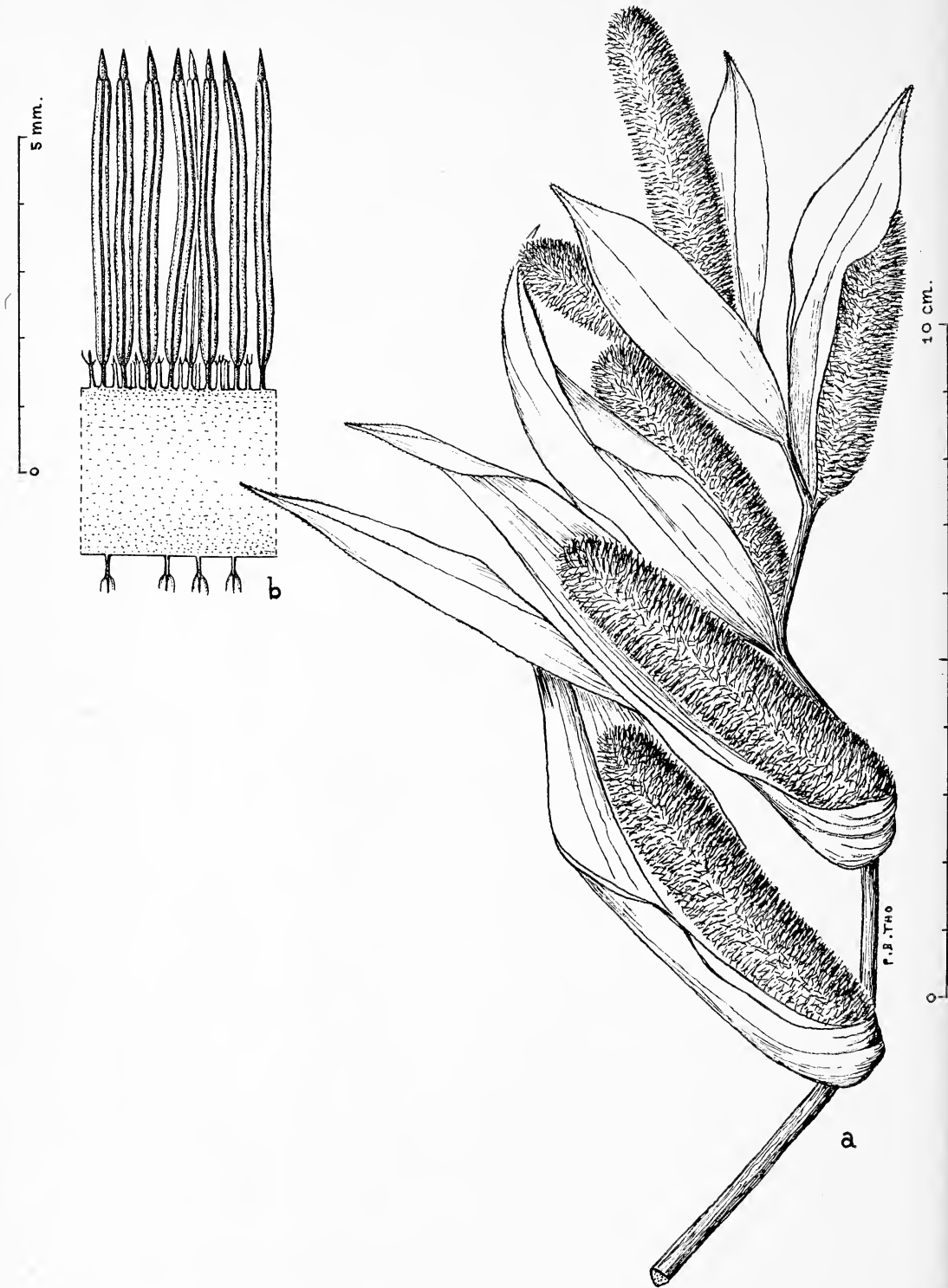


FIG. 221. *Pandanus recurvatus* St. John, from Johore, Ridley 12,143 (SING). *a*, staminate inflorescence,  $\times 1$ ; *b*, spike axis with stamens,  $\times 10$ .

margins with prickles 0.5–1 mm long, 4–11 mm apart, subulate, flat appressed ascending; along the outer third on the upper surface the two lateral pleats with subulate tipped serrations 0.3–0.5 mm long, 3–10 mm apart; on the caudate apex the margins and midrib below with serrations 0.3–0.5 mm long, those on the margins 1–2.5 mm apart, those on the midrib below 2–4 mm apart; pistillate inflorescence terminal, the tip pendent, bearing 1 syncarp (or rarely with 2–5 lateral, smaller, secondary ones); peduncle 20–52 cm long, 4–9 mm in diameter, 3-sided, bracteate; syncarp 12–23 cm long, 2.5–5.5 cm in diameter, cylindric, with obtuse ends, bearing 400–1,728 drupes, these 11–15 mm long, or following the curve of the style 13–18 mm long, 3–4 mm wide and thick, oblong-oblancoate, with a subulate apex, 4–6-angled, the body 9–14 mm long; pileus 2.5–4 mm high, obliquely conic, smooth, usually obscurely angled; style 3.5–5.5 mm long, subulate, sharply arcuate proximally, rigid; stigma 2–4 mm long, linear, distal, brown, papillose; endocarp centering in lower  $\frac{1}{3}$ , the walls 0.1 mm thick, stramineous; apical mesocarp semiorbicular, filled with parenchyma; basal mesocarp sparse, fibrous and fleshy.

**DESCRIPTION OF STAMINATE PLANT** (*Ridley* 12,143): Plant with similar leaves; inflorescence 25 cm long; the bracts colored (white?), subherbaceous; lowest floral bract with a colored base 6 cm long and a foliaceous prolongation 15 cm long, 18 mm wide, ligulate, tapering gradually into a subulate apex; median floral bract 9 cm long, 2 cm wide, lanceolate, unarmed elsewhere, but the tip with margins and midrib below with yellow serrulations 0.2 mm long, crowded; the 7–8 spikes 3–6 cm long, 10–12 mm in diameter, dense, having the odor of crushed leaves of *P. amaryllifolius*; stamens separate, attached directly to the rachis, filaments 0.2–0.3 mm long; anther 3.5–4 mm long, linear, bearing a subulate prolongation of the connective 0.5–0.6 mm long.

**HOLOTYPE:** Malaya, Perak, Taiping Hill, 1,000 ft elev, 17 Feb. 1907, *Md. Haniff & Md. Nur* 2,395 (SING)! Isotype (K)!

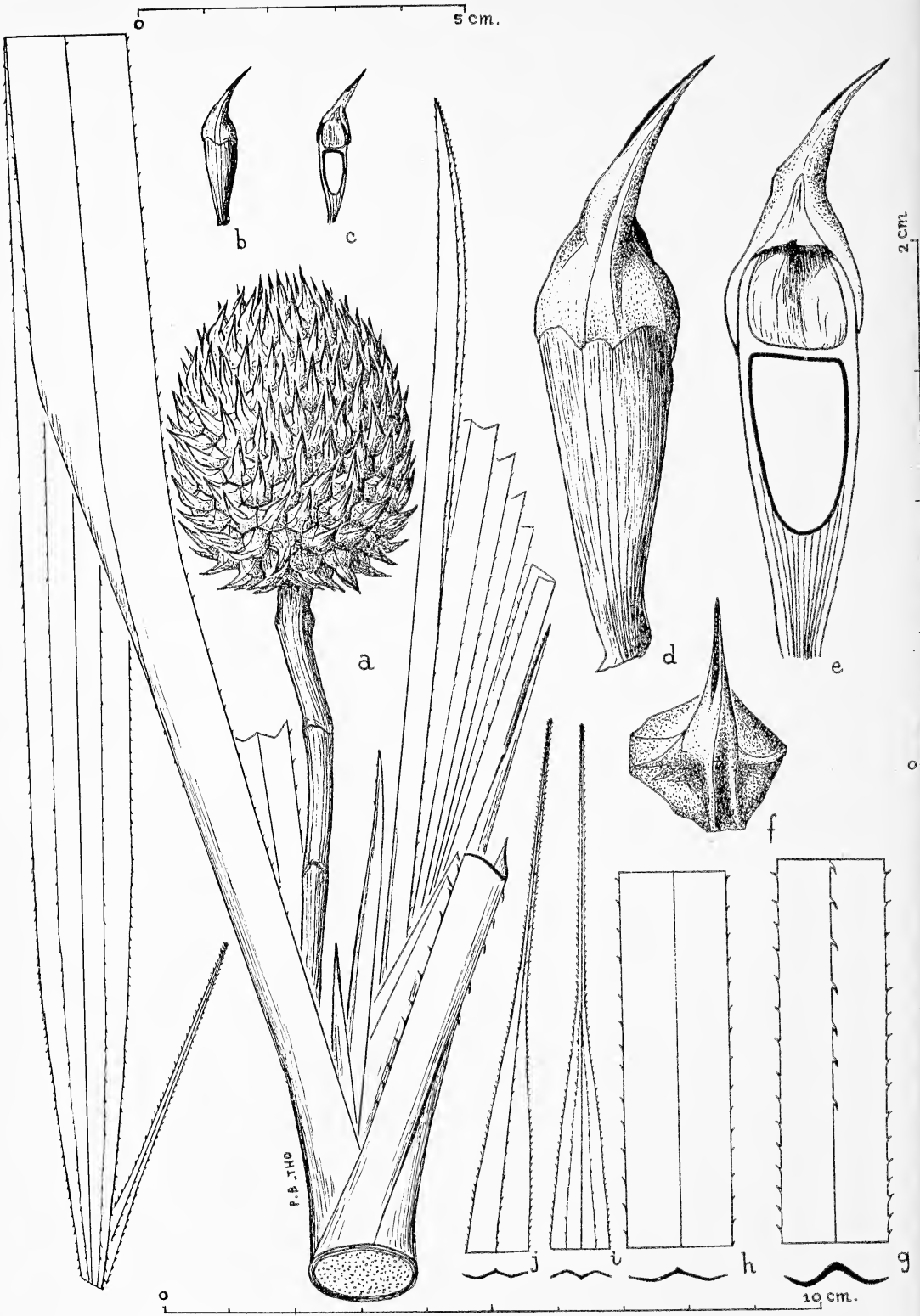
**SPECIMENS EXAMINED:** Malaya, Malacca, *Gaudichaud* (P), holotype of *Fisquetia ornata*

Gaud; also in (G), isotype; and (FI), clastotype; Malacca, without collector (FI); Perak, Larut, Gunong Boobo, 2,500–3,000 ft alt, March 1885, *H. Kunstler* 7,374 (FI); Sungei Penang Rd., 1,000 ft alt, Sept. 1887, *C. Curtis* 1,220 (K); Gunong Bintang, Kedah-Perak Boundary, June 1917, from Fed. Malay States Mus. (K); Tanjong Malim, 3 July 1924, *I. H. Burkill & Md. Haniff* 14,000 (K); Kedah, Koh Moi Forest Res., 5 April 1938, *Kiah* 35,190 (K); Penang, Government Hill, *Ridley* 2,272, type of *P. ornatus* f. *spicatus* Martelli (FI, K); Singapore, Bukit Timah, 1894, *H. N. Ridley* 6,287 (K); Johore, top of St. George, Gunong Pulau, Dec. 1905, *Ridley* 12,143 (K, SING), staminate; Trengganu, S. Trengganu Ferry, 26 April 1937, *E. J. H. Corner* 33,473 (K); Negri Sembilan, Tampin Hill, June 16, 1917, *Ridley* (K); Singapore, cult. in Bot. Garden, 1902, *Ridley* (FI); Johore, 2 miles N. E. of Kampong Sungei Sedili Besar, edge of forest at sea shore, 2 June 1962, *J. Sinclair* 10,703 (P); Kedah, Ulu Sungei Terenas, 20.3.1938, *Sow* 46,187 (KEP); Selangor, Ulu Gombak, 17.6.1931, *C. F. Symington* 24,534 (KEP); Kedah, Kedah Peak, 9.5.1938, *Symington* 46,937 (KEP); ditto, very common near top, 3,700 ft alt, 18/5/1957, *Wyatt-Smith* 79,292 (KEP).

Thailand: Bachaw, Pattāni, evergreen forest, 600 m alt, July 14, 1923, *A. F. G. Kerr* 7,191 (BK).

**DISTRIBUTION:** Throughout Malaya, near streams in lowlands and in forests on hills up to 3,000 ft alt; also in southern Thailand.

**Discussion:** *P. recurvatus* is a member of the section *Rykia*, as is its closest relative, *P. monotheca* Martelli, of Malaya, a species with the peduncle erect; syncarp 5 cm long, ovate-ellipsoid; drupes 10–13 mm long, obovoid or narrowly so, the body 7–9 mm long; pileus broadly ovoid; seed 4–5 mm long, obconic; leaves 0.7–1.1 m long, at midsection with 18 parallel secondary veins in each half, beginning 5 cm up from the base the margins with prickles 2–2.5 mm long, 2–5 mm apart, subulate sigmoid, and the lower ones recurving. *P. recurvatus* has the peduncle recurved; syncarp 12–23 cm long, cylindric; drupes 13–18 mm long, oblong-oblancoate, the body 9–14 mm long;



pileus obliquely conic; seed 9 mm long, narrowly ellipsoid, truncate; leaves 1.2–2 m long, at midsection with 27–31 parallel secondary veins in each half, and beginning 6–8 cm up the margins with prickles 1.5–2 mm long, 4–11 mm apart, subulate, ascending flat appressed.

*P. ornatus* Kurz forma *spicata* Martelli differs from the species only in having two small, lateral, secondary syncarps on the peduncle. This is considered to be a fluctuation within the limits of the species, and not a taxon worthy of classification or naming.

The new epithet is the Latin *recurvatus*, recurved, and is given with reference to the long, recurving peduncle.

*Pandanus ovatus* Warb., in Engler's *Pflanzenreich* IV, 9:80–81, 1900; *P. ovatus* (Gaud.) Kurz, *Asiat. Soc. Bengal, Jour.* 38(2):147, 1869, and *Flora* 52:451, 1869, an invalid name, not accepted by its author; *Fisquetia ovata* Gaud., *Bot. Voy. La Bonite, Atlas* t. 4, fig. 1, 1843, an invalid name published in an undescribed genus (sect. *Acrostigma*).

#### Fig. 222

**DESCRIPTION FROM ALL SPECIMENS EXAMINED:** Shrub, tufted, tussock-forming, or prostrate; stems to 50 cm long, pale brown, freely forking, at apex 11 mm in diameter; prop roots 4–6 mm in diameter, ridged, unarmed; leaves 73.5–120 cm long, 12–21 mm wide near the middle, firm chartaceous, green above, pale green below, 1-ribbed and deeply furrowed above along the midrib, 2-pleated and in section M-shaped, at midsection on each side with 20–21 parallel secondary veins, these prominent throughout, tertiary cross veins barely visible towards the base, but from the middle outward easily noted, forming elongate oblong meshes, the blade ligulate, but near the apex gradually narrowed to a 2–7 cm subulate, trigonous tip 0.3 mm wide, the base amplexicaul and unarmed, beginning at 3–3.5 cm up the margins with prickles 1.3–1.6 mm long, 3–6 mm apart, subulate, pale, divergent ascending; the midrib below beginning at 6.5–8.5 cm with prickles 1–1.5 mm long, 5–10 mm apart, horn-

like, reflexed; at midsection the margins with prickles 0.5–1 mm long, 2–4 mm apart, subulate, ascending; the midrib below unarmed; in the outer third on the upper surface the 2 lateral pleats bearing prickles 0.5–0.8 mm long, 2–6 mm apart, stout arcuate subulate, ascending, attached either on secondary veins or in the interval between them; on the subulate apex the margins and midrib beneath with prickles 0.3–0.5 mm long, 1–2.5 mm apart, subulate, ascending; pistillate inflorescence terminal, erect, bearing one syncarp; peduncle 6–13 cm long, 4–5 mm in diameter, 3-sided, bracteate; syncarp solitary, 4.5–5.5 cm long, 2–4.3 cm in diameter, broadly ellipsoid to globose, green, with 240–320 drupes, these 21–23 mm long, 4–5 mm wide and thick, fusiform but the tip more slender, 5–7-angled, the body 10–11 mm long, oblanceoloid, obtuse; pileus 9–12 mm long, the base 5–6 mm high, pyramidal-semi-orbicular, with 5–7 prominent angles, smooth; style 6–9 mm long, all but the apical ones curved proximally, slightly angled at base, then subterete; stigma 3–5 mm long, broadly linear, dark brown, papillose, distal, running almost to the tip; endocarp in lower  $\frac{1}{3}$ , inverted bullet-shaped, the walls 0.2 mm thick, bony, stramineous; apical mesocarp 4 mm long, a single cavern, depressed barrel-shaped, with a few large, longitudinal white membranes; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** *Fisquetia ovata* Gaud., the illustration in *Bot. Voy. La Bonite, Atlas*, t. 4, fig. 1, 1843 which was drawn from the specimen, Malacca, *Gaudichaud* (P). Also there is a clastotype of 12 loose drupes (F1). Specimens examined! Also an isotype (G)!

**SPECIMENS EXAMINED:** Malaya, Kelantan, Sungei Kete, 7 Feb. 1924, *Md. Nur & Foxworthy* 11,988 (SING); Pulo-Pinang [= Penang], *Voyage de la Bonite, mars* 1837, *Gaudichaud* (G-DEL); Kedah, Tampoi For. Res., secondary forest, very common, 200 ft alt, 2/3/1960, *Y. K. Wong* 94,253 (KEP).

FIG. 222. *Pandanus ovatus* Warb., from Sungei Kete, *Nur & Foxworthy* 11,988 (SING). *a*, fruiting branch, lateral view,  $\times 1$ ; *b*, drupe, lateral view,  $\times 1$ ; *c*, drupe, longitudinal median section,  $\times 1$ ; *d*, drupe, lateral view,  $\times 4$ ; *e*, drupe, longitudinal median section,  $\times 4$ ; *f*, drupe, apical view,  $\times 4$ ; *g*, leaf base, lower side,  $\times 1$ ; *h*, leaf middle, lower side,  $\times 1$ ; *i*, leaf apex, upper side,  $\times 1$ ; *j*, leaf apex, lower side,  $\times 1$ .

**DISTRIBUTION:** Occurring generally throughout the lowland parts of Malaya.

**DISCUSSION:** Gaudichaud published illustrations and binomials for his four species of *Fisquetia*, but did not describe the genus. Hence, all of these species are invalid and cannot even be transferred.

Kurz transferred Gaudichaud's species to *Pandanus*, but in an uncertain way. In treating the section *Acrostigma* he said, "*P. ovatus* (*Fisquetia ovata*, Gaud., loc. c., t. 4, fig. 1) seems to belong to this section." To the species which he accepted he gave consecutive numbers and printed their binomials in bold face. His *P. ovatus* was left unnumbered and was printed in italics, and he said, "it seems to belong to this section." So, he did not positively accept it. Gaudichaud's species could not be transferred, and Kurz failed to provide a description for it.

Gaudichaud's figure (Voy. La Bonite, Atlas t. 4, fig. 1, 1843) was a large drawing of a leafy branch with syncarp. He made no drawings of the drupes, though he had good fruiting material. His habit drawing is in general good, except that the leaf prickles were shown as too large, too regular, and too close together.

*Pandanus spurius* Miq. cv 'PUTAT' cultivar nov. (sect. *Pandanus*).

*P. moschatus* seu *laevis* Rumph., Herb. Amb. 4:147, 1743.

*P. moschatus* Rumph. ex Miq., Fl. Ind. Bat. 3:165, 1855.

*P. tectorius* Sol., var. *moschatus* (Rumph. ex Miq.) Merr., Interp. Herb. Amb. 81, 1917.

*P. laevis* Lour., Fl. Cochinch. 2:604, 1790, in part, this based on *P. laevis* Rumph. (1743) and on Indochinese plants, part *Corypha*, part *Pandanus*, typified on the Rumphius plant from Amboina, Java, a cultivated plant, sterile, with unarmed leaves, by Kunth, Enum. Pl. 3:100, 1841; later typified by Merrill (1935) on the Indochinese plants described by Loureiro, not yet identified, but incorrectly so, since Kunth

(1841) had already typified it upon a permissible choice (see Merrill, Interp. Rumph. Herb. Amb. 81, 1917).

*P. tectorius* Sol. var. *laevis* (Kunth) Warb., Engler's Pflanzenreich IV, 9:48, 1900.

*P. odoratissimus* L. f. var. *laevis* (Warb.) Martelli, Bishop Mus., Occas. Papers 10(13):21, 1934.

*P. inermis* Roxb., Fl. Ind., ed. Carey, 3:744, 1832.

*P. laevis* Rumph. ex Kunth, Enum. Pl. 3:100, 1841.

*P. laevis* Rumph. ex Willd., Linnaeus, Sp. Pl. ed. by Willd., ed. 4, 4:646, 1805.

*P. laevis* Rumph. ex Solms, Linnaea 42:61, 1878.

*P. tectorius* Sol. forma *laevis* (Kunth) Warb. ex Masamune, Kanazawa Univ., Fac. Sci. Repts. 4(2):202, 1956.

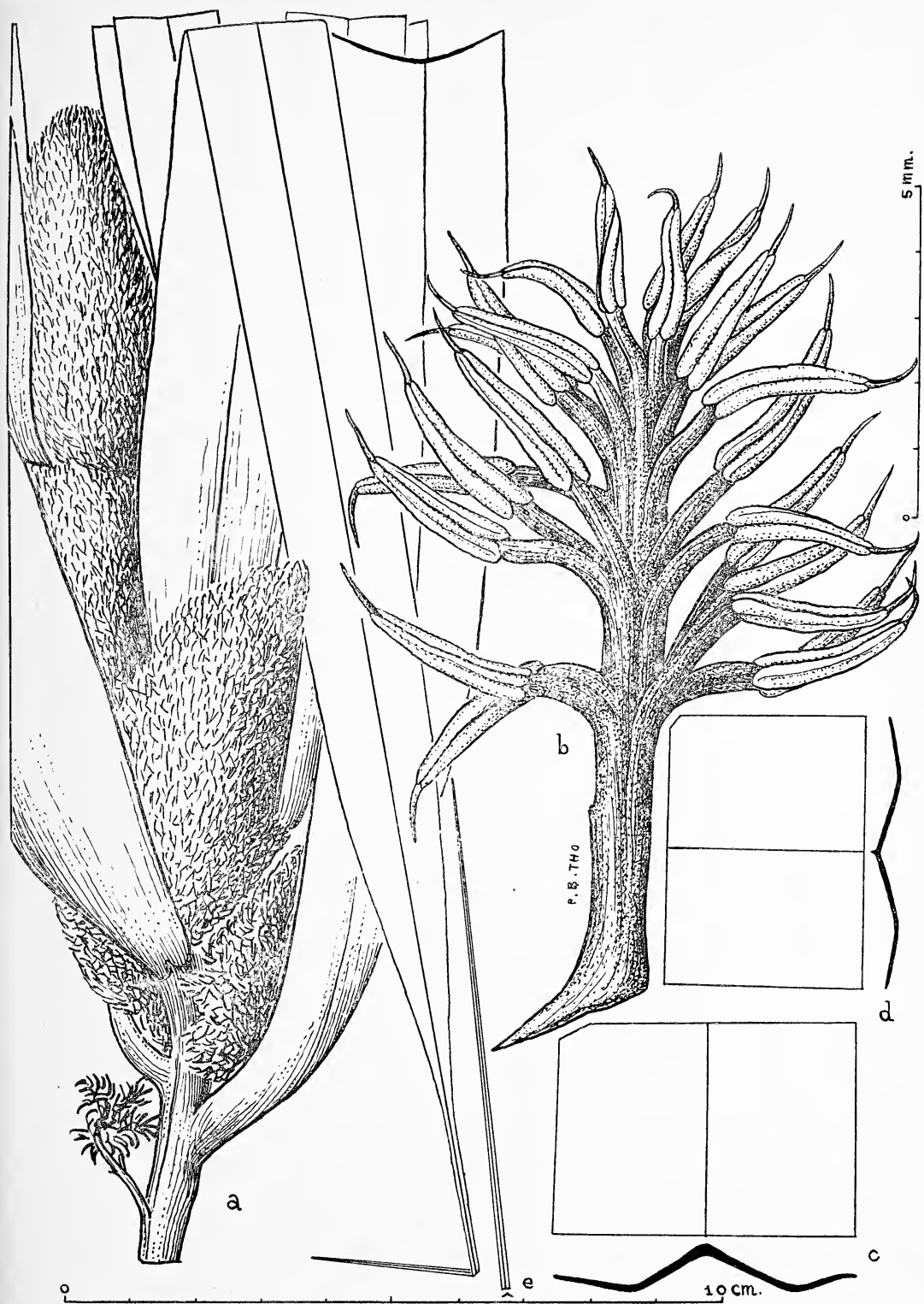
#### Fig. 223

NOM. VERN.: "putat" (Java); "pudak" (Sundanese).

**DESCRIPTION** (from Singapore, Corner 32, 763): Forming a tuft 4 m tall; stems silvery buff, shaggy with old leaf bases; prop roots several; leaves 1.43 m long, 4.5 cm wide, completely unarmed, furrowed above the midrib, at midsection with 48 parallel secondary veins in each half, tertiary veins visible below, making square or oblong meshes, coriaceous, green, not glaucous, blade sword-shaped, gradually tapering to a 30–40 cm subulate, trigonous caudate apex, this at the point 10 cm down 1.3 mm wide, the base broadened, amplexicaul; staminate inflorescence 40–70 cm long, drooping, with many creamy yellow bracts, fragrant, the lowest floral bract with a narrowly lanceolate body 30 cm long, 3.5 cm wide, herbaceous, yellow, bearing an apex 51 cm long, narrowly lanceolate, foliaceous, with a long subulate apex; median floral bract 30 cm long, 2.2 cm wide, narrowly lanceolate, herbaceous, unarmed; staminate spikes about 12, cylindric, 4–5 cm long, 1.5–2 cm in diameter, dense; stamens in fascicles 8–12 mm long, with 21–29

FIG. 223. *Pandanus spurius* Miq. cv. 'PUTAT,' from holotype. a, staminate inflorescence, lateral view,  $\times 1$ ; b, fascicle of stamens,  $\times 10$ ; c, leaf base, lower side,  $\times 1$ ; d, leaf middle, lower side,  $\times 1$ ; e, leaf apex, lower side,  $\times 1$ .





anthers; column 6–9 mm long, anther bearing on upper  $\frac{2}{3}$ 's; free filament tips 1–2 mm long; anthers 1.6–2.2 mm long, narrowly lanceoloid, auriculate at base, bearing at the apex a subulate projection of the connective 0.6–0.9 mm long.

HOLOTYPE: Singapore, Kampong Tanjong, Labrador, cult. for making of mats, 11 March 1937, E. J. H. Corner 32,763 (SING). Iso-type (K)!

SPECIMENS EXAMINED: all in staminate flower.

Java: Hort. Bogor (CAL, L); ex hort. Bogor (CAL); cult. Mus. Heyne, Batavia (L); cult. Museumtuin no. 24 (L); Java, W. H. de Vriese (L); without data (CAL); without data, "puedak" (CAL).

India: H. B. C. (Hortus Botanicus Calcuttensis), (CAL, K); H. B. C., Griffith 6,365 (K); ditto, Wallich 8,589 (K). Without Locality: 1867, Teysmann (L).

DISCUSSION: The above specimens from Java apparently represent *P. moschatus* Rumph. ex Miq., and those from India were the basis of *P. inermis* Roxb.

It is apparent from the habit and from the staminate flowers that this is a member of the section *Pandanus*. The main problem is to decide on the species. It is a plant cultivated by the native peoples from southeastern Asia to the extremes of Polynesia. It is the preferred sort for the making of mats, due to its bland, unarmed leaves. It is mostly sterile, perhaps due to the weakening effect of continual leaf harvests. The natives say that it never bears fruit. Rarely, larger, older plants bear male flowers, as does the Corner 32,763 specimen here described. So, it is a variant, always propagated vegetatively. It appears to have started as a bud sport on a staminate plant of some species of the section *Pandanus*. The staminate flowers of all species in this section are very similar, but only a small percentage of them are described and completely known. The leaves, lacking the spines, are not sufficiently distinctive to help in the specific determination. Earlier botanists described it as a species, then as a variety, under several names, and attached it to several

species. Upon the assumption that all littoral *Pandanus* belonged to a single species, it was attached to either *P. tectorius* Soland. or to *P. odoratissimus* L. f.

It is evident that it is not a species. Probably it is not a hybrid. With little doubt it is a bud sport obtained millenia ago from some wild species. Its current classification should surely be that of a cultivar, and as such it should be attached to a species.

The author now attaches this cultivar to *P. spurius* Miq., a species also native to Amboina. It is of the same section *Pandanus*, and has been well figured and described. Though long misunderstood by botanists who had no specimens, it is now represented by several collections from Amboina in the herbarium at Firenze. In a subsequent part of this revision the writer will present new figures and an expanded description, in order to make *P. spurius* better known. We have not proved that the cv 'PUTAT' was derived from *P. spurius*, but they are of the same section, occur in the same region, and on the same shores and inhabited lowlands. The Ambonese people have long used the leaves of *P. spurius* for matting. If, long ago, they found a spineless bud sport, it is likely that they would have preserved it and multiplied it by stem cuttings.

The name here given to this cultivar is 'PUTAT,' the vernacular name on Java (*vide* Rumphius), now as "pudak," the Sundanese vernacular name (*vide* Koorders).

The classification of this cultivated variety is difficult, and previous botanists have given it many placements. The first good account and naming of this plant was by Rumphius (1743) who gave it the alternative names *P. moschatus* seu *laevis*, but he himself actually accepted *P. moschatus*. In post-Linnaean literature this was validated as *P. moschatus* Rumph. ex Miq. (1855); and as *P. tectorius* Soland. var. *moschatus* (Rumph. ex Miq.) Merr. (1917).

The alternative name given by Rumphius was also republished and validated as *P. laevis* Lour. (1790); as *P. laevis* Rumph. ex Willd (1805); as *P. laevis* Rumph. ex Kunth (1841); as *P. laevis* Rumph. ex Solms (1878); as *P. tectorius* Soland. var. *laevis* (Kunth) Warb. (1900); as *P. tectorius* Soland. forma *laevis*

(Kunth) Warb. ex Masamune (1956); and as *P. odoratissimus* L. f. var. *laevis* (Warb.) Martelli (1934). The first of these, *P. laevis* Lour. was published as a new species, not attributed to Rumphius. Loureiro included a reference to *P. laevis* Rumph. and his description was in part from Cochinchinese plants of *Pandanus*, and with vernacular names of palms in *Corypha*. This was first typified by Kunth (1841) on the Rumphian plants of Amboina. Hence, later interpretations, as that by Merrill, that *P. laevis* Lour. must be applied to the obviously different *Pandanus* seen in Vietnam by Loureiro, were superfluous and illegal. Kunth had already made a possible and legal typification of the species. Nor can combinations based upon *P. laevis* sensu Kunth be used, since he had no independent species, and if he had, it would have been a later homonym of the one by Loureiro. It is possible to use the name *P. tectorius* Soland. var. *laevis* Warb. (1900), as var. *laevis*. Warburg could not legally transfer and adopt *P. laevis* sensu Kunth, but in fact Warburg gave a Latin diagnosis and cited specimens, so var. *laevis* has a legitimate beginning with Warburg in 1900.

Warburg also cited as synonyms *P. moschatum* s. *laevis* Rumph. and *P. moschatum* Miq. For localities he listed Java, Bali, and Amboina; and quoted Kurz as finding it at Pegu. In the Berlin herbarium there are no such specimens, and the only ones there, and annotated by Warburg, are two from Calcutta, one collected by Guadichaud in Hortus Calcutt. and sent to Kunth in 1841, and the other Herb. Wallich 842B. These contain only staminate inflorescences. Since in preparing his monograph Warburg studied only the specimens in the Berlin museum, it is evident that he based his concept of this plant upon published descriptions, not upon actual specimens.

*P. inermis* Roxb. is a valid name, based upon plants from Amboina cultivated in the Calcutta Botanic Garden. In 1961 this plant was no longer present in the Calcutta Garden, but there were two sheets with male inflorescences so labeled in the Calcutta herbarium and they match the material from Singapore here described as a new cultivar.

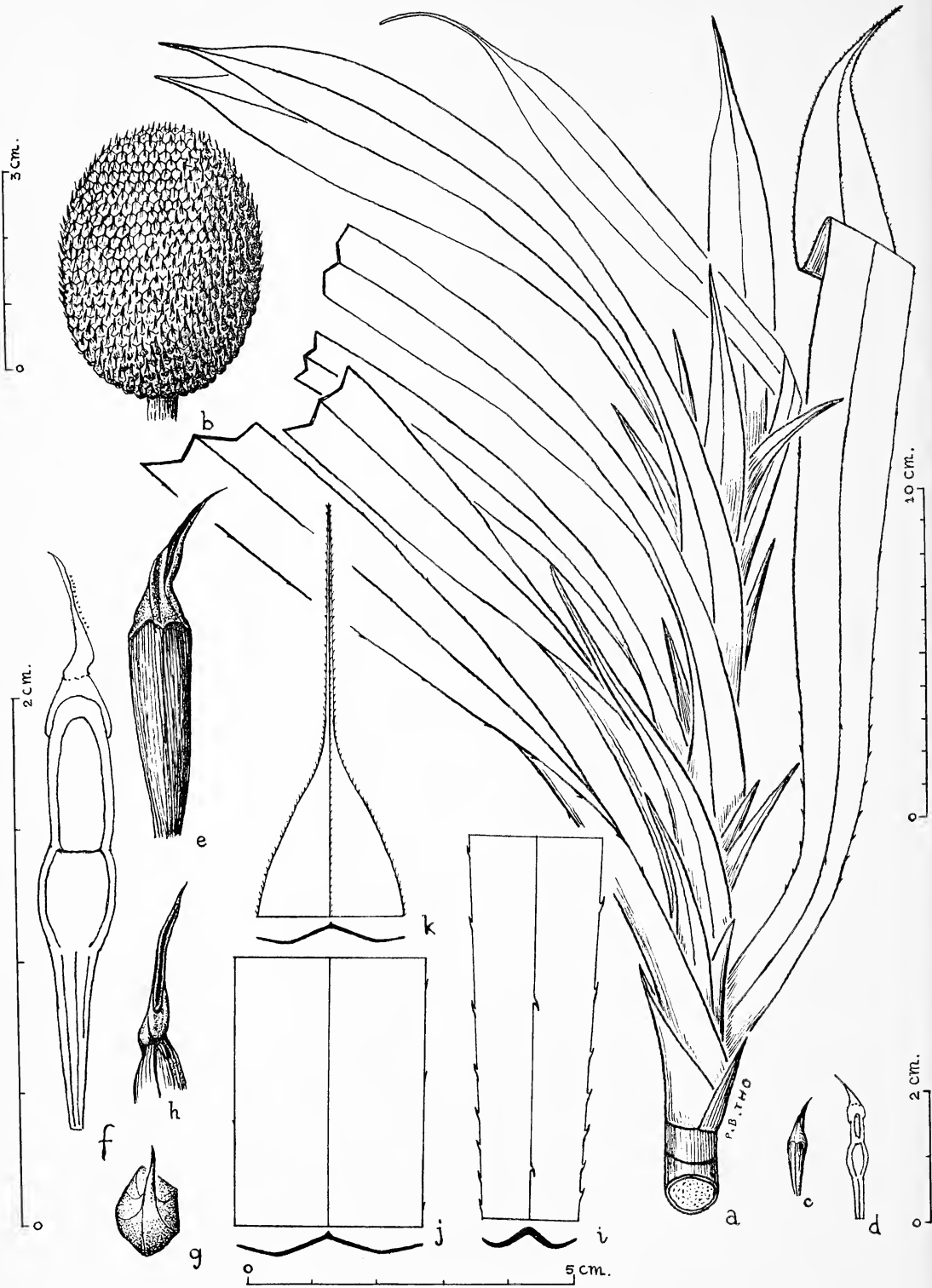
Another complication is that *P. tectorius*

Soland. was merely a manuscript name with an unpublished figure until it was adopted by Warburg in 1900. He gave other references to subsequent authors, but none of these used the name *P. tectorius*. So Warburg himself was the first to print a diagnosis, cite specimens and references. Hence, *P. tectorius* Warb. (1900) is an acceptable name for a Tahitian species, but it is no longer a usable mother species to which all other littoral kinds can be appended as varieties. There are many other older species of the section *Pandanus* which have priority over the binomial by Warburg. Since the writer does not accept this sort of classification, the wholesale grouping of all littoral kinds of *Pandanus* under one species, he is not concerned with which would be the earliest possible collective species for all littoral *Pandanus*. The publication of *P. tectorius* is often attributed to S. Parkinson's Journal (1773), but in this posthumous, non-technical book, the name was printed as a monomial, and hence is invalid.

*Pandanus Scortechinii* Martelli, Soc. Bot. Ital., Bul. n. s. 11(2):302, 1904, (as *Scortechinii*), emended to *Scortechinii* by Martelli, Webbia 4(1):30, 78, 96, 1913; and 4(2):t.34, fig. 12-15, 1914 (sect. *Rykia*).

Fig. 224

DIAGNOSIS OF LECTOTYPE: Pistillate plants with the stem 60-120 cm tall, 13 mm in diameter, yellowish, smooth, shining; leaves 25-33 cm long, 1.9-3.1 cm wide near the middle, 1.4 cm wide near the base, thick chartaceous, only the midrib thickened, but the blade 2-pleated, cuneate to near the expanded, unarmed base, the midsection almost ligulate, then near the tip suddenly contracted to a caudate, subulate, trigonous apex 3 cm long, this 2 cm down 1.3 mm wide, the blade 1-ribbed, but pleated and in section M-shaped, above dark green, below paler, the secondary parallel veins conspicuous and at midsection 15-16 in each half, below in outer half the tertiary cross veins visible, almost transverse, making squarish meshes, beginning at 3-4 cm from the base the margins with prickles 2-2.3 mm long, 3-6 mm apart, subulate, ascending, brown tipped; the midrib below beginning at 5-6 cm up with 1-2 reflexed serrulations 0.5-1 mm long, and if two 19 mm



apart; at midsection the margins with weak prickles 0.2–0.3 mm long, flat appressed, ascending, close or remote or none; the midrib below unarmed; on the caudate apex the margins with teeth 0.3–0.7 mm long, 1–1.5 mm apart, subulate tipped serrulations; the midrib below with similar ones but 1–3 mm apart; syncarp 4–5 cm long, 3–3.5 cm in diameter, erect, single, oval; drupes numerous, 12–22 mm long, 1.5–3 mm wide and thick, oblong-fusiform, 4–6-angled, the body 7–18 mm long; pileus 2–3 mm high, ovoid; style 4–5 mm long, subulate from a broad, compressed base, pale, cartilaginous; stigma 2.5–3 mm long, proximal, linear, not reaching the apex, brown, papillose; endocarp in lower  $\frac{1}{3}$ , cartilaginous, the walls stramineous, 0.1 mm thick, 6 mm long, ellipsoid but smaller towards the base; seed 3 mm long, ellipsoid; apical mesocarp a slender ellipsoid cavern 5–6 mm long; basal mesocarp with fibers up the sides, the center fleshy but when dried hollow.

LECTOTYPE: Malaya, Perak, Larut, to 300 ft alt, 1882, *Dr. King's Collector* 3,557 (CAL)! Isotype (SING)! and (FI)!

SPECIMENS EXAMINED: Malaya, Dindings [= Perak], new road from Bruas to Sungei Rotan, Feb. 1900, *C. Curtis* (SING); Perak, Larut, very wet places, rich soil, dense jungle, 300 ft alt, June 1882, *H. Kunstler* 3,085 (CAL); without locality, *Scortechinii* (CAL); plains, Kota, Oct. 1888, *L. Wray Jr.* 3,260 (CAL); Kota, Thaiping, plains, Oct. *L. Wray Jr.* 5,797 (SING).

DISCUSSION: *P. Scortechinii* is a member of the section *Rykia*. It was briefly described by Martelli only in a key. This was valid publication but regrettably brief. He based his new species upon collections from Malaya and upon three collections by Wray from Assam in northern India. Later Martelli restricted the area of his own species, as in his enumeration (*Webbia* 4(1):30, 1913) he listed it as an accepted species and gave its occurrence only as "Penis. Males." Thus, Martelli by implication excluded the specimens from Assam, which the writer is now separating as a new species. Of the several collections from Malaya, the one from Larut, *Dr. King's Collector* 3,557, is here designated as lectotype.

FIG. 224. *Pandanus Scortechinii* Martelli, from isotype (SING). *a*, leafy branch, lateral view,  $\times \frac{1}{2}$ ; *b*, syncarp, lateral view,  $\times 1$ ; *c*, drupe, lateral view,  $\times 1$ ; *d*, drupe body, longitudinal median section,  $\times 1$ ; *e*, drupe, lateral view,  $\times 4$ ; *f*, drupe body, longitudinal median section,  $\times 4$ ; *g*, drupe, apical view,  $\times 4$ ; *h*, pileus, style, and stigma, lateral view,  $\times 4$ ; *i*, leaf base, lower side,  $\times 1$ ; *j*, leaf middle, lower side,  $\times 1$ ; *k*, leaf apex, lower side,  $\times 1$ .

# Weight Variation in Adrenal Glands of the Mongoose in Hawaii

P. QUENTIN TOMICH<sup>1</sup>

**ABSTRACT:** Gross morphology and weight characteristics are described for adrenal glands in a population of the small Indian mongoose, *Herpestes auropunctatus* (Hodgson). Mongoose adrenals are anatomically similar to those in the cat and dog, and may be typical of those in the Order Carnivora. The right gland is about 80% as large as the left. Relative adrenal weight decreases in all age and sex classes as body weight increases. Adrenals are only slightly larger in young females than in young males, but at sexual maturity they enlarge greatly in females and remain much larger than those in males. In lactating females the adrenals are significantly larger than those in all other classes of adult females. There seems to be no major effect of sexual maturity on adrenal size in males. Over a three-year period the population demonstrated a remarkable stability of adrenal gland weight in the face of increasing drought and decreasing numbers. Minor adrenal response to seasonal fecundity, environmental stress, and variations in population density may be a character of carnivores quite in contrast to that observed in the highly sensitive rodents.

THERE HAVE BEEN two recent analyses of how the pituitary-adrenocortical-gonadal system effectively regulates growth and decline of free-living mammalian populations. Christian (1961) emphasizes the intrinsic mechanisms of density and social interaction as the indirect effectors of population control. Negus, Gould, and Chipman (1961) attribute this regulation primarily to the extrinsic factors of climate and nutrition. Further progress in understanding adrenal gland function as it applies to population theory depends in part on a clearer knowledge of adrenal form and size patterns as they occur in the several orders of mammals.

This report on the small Indian mongoose, *Herpestes auropunctatus* (Hodgson), increases what is known about the carnivores, which have apparently been omitted from population studies dealing with the adrenals. The mongoose was introduced into Hawaii in 1883 from stocks earlier transplanted to Jamaica from India, and it became rapidly established on four of the main islands.

## METHODS

Samples of mongoose adrenals were collected monthly in Hamakua District on Hawaii Island between April, 1960 and March, 1963 during ecological studies of the reservoirs and vectors of bubonic plague. The mongooses were trapped alive, killed with CaCN dust, taken to the laboratory and weighed. Adrenals were removed, trimmed of adherent tissue, and preserved (in 10% neutral formalin, except for a small number of those collected in the third year, which were placed in Bouin's fluid). After fixation each pair of glands was blotted on paper towel and weighed immediately on a torsion balance to an accuracy of 0.1 mg. Weights were then expressed in milligrams per 100 grams of body weight (mg%), and are presented throughout the report in this relationship.

For statistical analysis the 36 monthly samples comprising 784 pairs of adrenals were sorted according to age, sex, and reproductive state of the individual mongoose. Age classes were two: immature and adult. Males with the bare testes less than 8 mm long were classed as immature (and hence sexually inactive), and all others were considered adult; criteria were approximately those of Pearson and Baldwin

<sup>1</sup> Plague Research Unit, State Health Department, Honokaa, Hawaii. Manuscript received January 29, 1964.

(1953). Females were classed as immature if non-parous and inactive, and as adult if in any stage including and following first onset of uterine enlargement. Adult females were subdivided into four classes: active (preimplantation), pregnant, lactating, and inactive, in the sequence of the breeding cycle.

Analysis of variance by the approximate method of unweighted means (Snedecor, 1956: 385–386) was the principal test applied. The more sophisticated method of fitting constants (Steel and Torrie, 1960: 257–265) was used to determine levels of significance between years in the combined classes. Duncan's new multiple range test (Steel and Torrie: 107–109) extended the usefulness of both these methods.

### ANATOMICAL DESCRIPTION

Mongoose adrenal glands are quite regular in shape, lacking the acutely angular borders, prominent notching, and frequently bi-lobed appearance of these glands in the dog as figured by Baker (1936). The left gland is somewhat elongate and flattened compared to the right one, which is often blunt and thick with slightly angular lateral and ventral borders. Both glands tend to narrow toward the posterior end. They lie closely against the dorsal body wall just medial to the anterior poles of the kidneys. The right gland is nearly concealed by the postcaval vein, and this seems to enhance its medio-lateral depression and to form the angular borders described. The caudate lobe of the liver envelopes the free surfaces of this gland, the lateral surface in particular, and intensifies its crowded position. The left gland is freely situated; it lies adjacent to the postcaval vein and is lightly pressed against the dorsal body wall by the pancreas and stomach.

One adrenolumbar vein courses along the anterior and dorsolateral surfaces of the right adrenal, and receives a prominent branch from its anterior quarter. The other arches across the posterior ventral third of the left adrenal, receives a branch from this gland, and frequently impresses a slight notch in its medial border where the vessel enters the left renal or the postcaval vein.

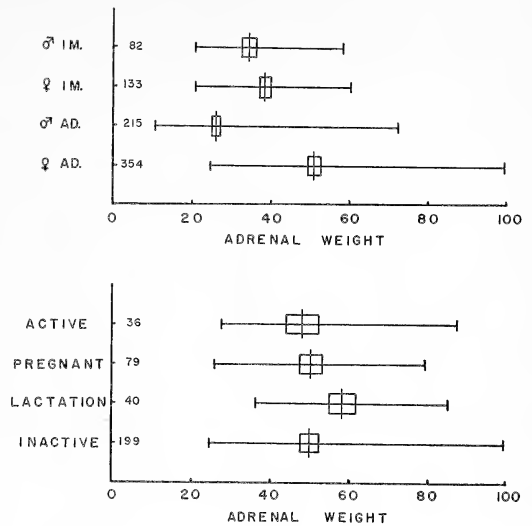


FIG. 1. Mongoose adrenal weights in milligrams per 100 grams of body weight, according to age and sex (*above*), and for the adult females classed by reproductive condition (*below*). Means plus and minus two standard errors, extremes, and sample size are indicated for each class.

The right adrenal is smaller than the left one, as in most mammals. The mean weight of the right gland in a series of 20 males was  $79.3 \pm 0.53\%$  (1 SE) of the left one, and in 20 females it was  $79.7 \pm 0.66\%$  ( $P < 0.01$  in both sexes between right and left glands).

### RESULTS

In young males (Fig. 1) the mean relative adrenal mass is slightly smaller than in young females ( $P < 0.05$ ). In adults this divergence is intensified: for males relative mean gland size becomes even smaller, and for females it becomes much larger ( $P < 0.01$  in comparisons of adults of each sex with all other classes). Seasonal fluctuations in adrenal size are small in adults. Among females (Fig. 1) significant change occurs only in lactation, when size is greater than in any other adult class ( $P < 0.01$  for each). Testes of adult males regress only slightly in the non-breeding period, approximately from August through December. In a sample of 126 males older than one year, as judged by progressive toothwear, I found no significant differences in adrenal size between



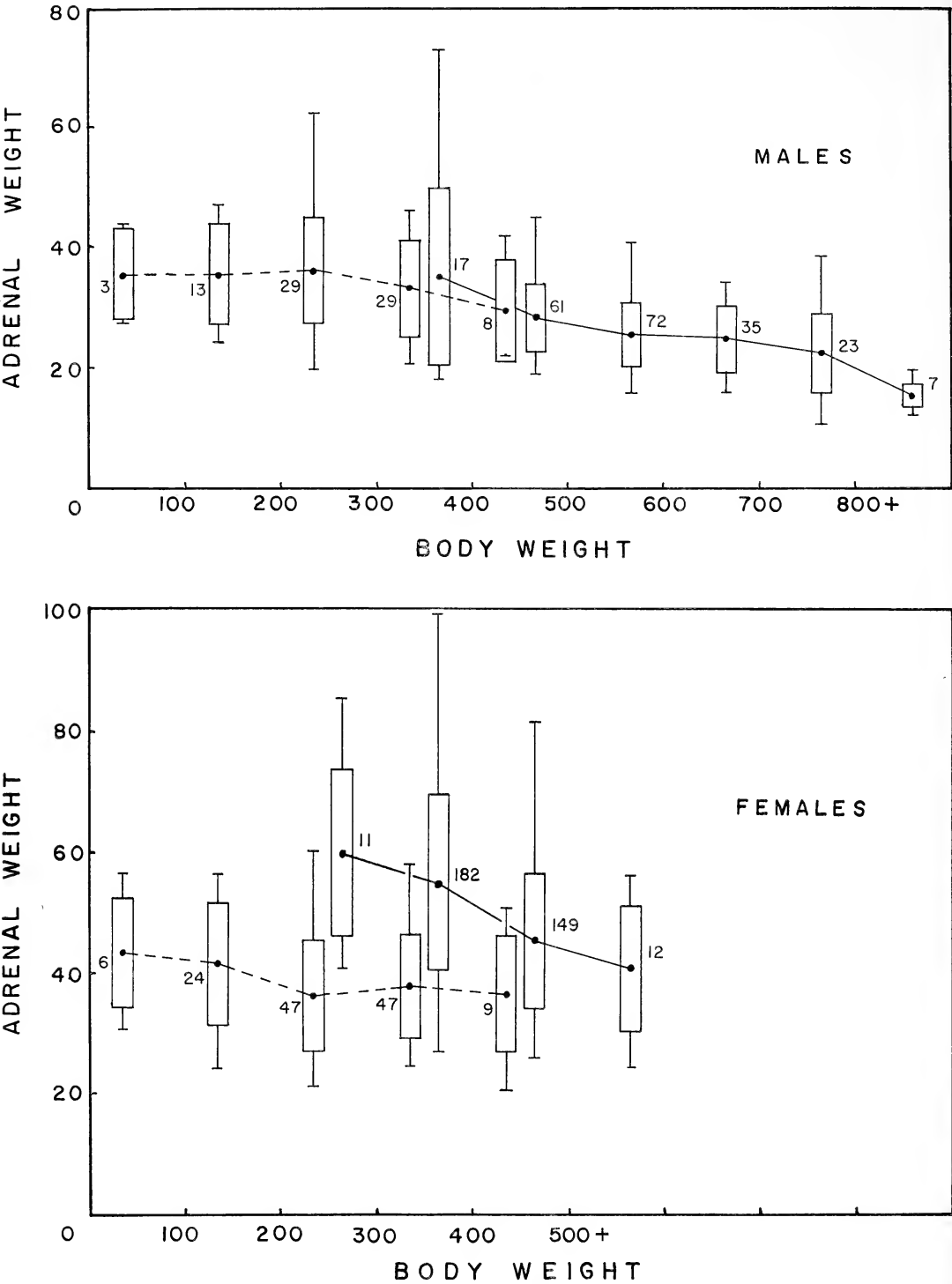


FIG. 2. Adrenal weights of mongooses in milligrams per 100 grams of body weight plotted against body weight. Means plus and minus one standard deviation, extremes, and sample size are indicated for each 100-gram class. Solid lines connect means of adult classes; dashed lines connect means of immature classes.

TABLE 1

ADRENAL SIZE (IN MG/100 G BODY WT) IN ADULT MALE MONGOOSES BY SEASON

SEASON	NUMBER	RANGE	MEAN	SE
Breeding (Jan.-July).....	86	11.9-62.3	27.9	$\pm 0.76$
Nonbreeding (Aug.-Dec.).....	40	14.1-52.9	25.7	$\pm 1.73$

those taken in the breeding season and those taken after it (Table 1).

As body weight of males increases there is an almost continuous trend in reduction of relative adrenal weight (Fig. 2). The transition to adulthood is smooth, showing that adrenal size is not greatly influenced by sexual maturity. In contrast, although the trend in young females matches closely that in young males, adult females demonstrate an explosive increase in adrenal size. Once this increase is established, the mean trend in its reduction as body weight increases covers almost the same amplitude as that in adult males (though distributed over four weight range classes instead of six).

In the advanced fetus, adrenal glands are noticeably large and their relative weights exceed those of all other age classes examined ( $P < 0.01$ ). Three fetuses near term and averaging 20.1 g in body weight had a mean relative adrenal mass of  $125.0 \pm 11.4$  mg % (1 SE).

#### DISCUSSION AND CONCLUSIONS

The cat (Northup and Van Liere, 1960) has a slightly larger adrenal mass in adult females than in adult males, and in smaller members of both sexes than in the larger ones. Baker (1936) examined 1250 dogs of a wide variety of breeds and ages, and found conditions in immature animals similar to those which I found in the mongoose. When body weight of dogs increased, relative adrenal weight decreased in all classes; but, as in cats, adult females had only slightly larger adrenals than did adult males. This may be related to the status of both these species as domestic animals. Among wild species the basic pattern of adrenal weight variation in the vole, *Microtus*

*montanus* (McKeever, 1959), is similar to that in *Herpestes auro-punctatus*, although in the vole prominent seasonal variation occurs as it does in most short-lived rodents, and this is not found in the mongoose.

Mongoose used in this study were collected in a period of almost continuously subnormal rainfall and increasingly serious drought conditions. The moderately dense population decreased markedly in most sections of the district (Tomich, MS). Yet no significant differences were observed in adrenal size among the three years within any of the age and sex classes (Table 2). The female reproductive stage classes were likewise remarkably uniform in the three years, and also showed no significant differences (Table 3). Statistical interaction was not evident.

This rigid stability within the various classes may be interpreted in terms of stress theory to mean that environmental and sociological effects were actually slight and easily accommodated, or that the mongoose is refractory in the nature of its pituitary-adrenocortical-gonadal system to effects commonly measureable in rodents. Fat is not a complicating factor in these relationships because few animals had fat deposits and these deposits were seldom large.

Unexpectedly, there was within each class a downward trend by years in mean adrenal values (see Table 2). In the first year (all classes combined) adrenals were larger than in the two succeeding years ( $P < 0.01$  for each). The implication of this observation is that a normally wet year with a high population was less favorable to the mongooses than the following dry years with a reduced population. In view of the generally slight adrenal response within the various classes, I prefer to withhold judg

ment on this matter until further evidence is available.

McKeever (1959) reviewed the effects of reproductive hormones on adrenal size in mammals, stating that in general androgens decrease, and estrogens increase, thickness of the adrenal cortex, and that this results in changes in adrenal weight. These effects are suggested by data on the mongoose because of the gradual reduction of relative adrenal size in the maturing male and its sudden enlargement once the female is adult.

Histological study (McKeever and Tomich, 1963) confirms the above observations and reveals an inner zona fasciculata in adrenals of adult female *Herpestes auropunctatus* which accounts in part for the large cortical width in that class. This subzone reaches its greatest development during lactation, when cortical width and adrenal weight are at a maximum.

The implications of adrenal size patterns as they vary in the several orders of mammals are not completely elucidated by available data. At least some lagomorphs are unlike the carnivores; in both *Oryctolagus* and *Sylvilagus* adrenals of all age groups are larger in males than in females, about 40% heavier when considering all

age classes together (Wodzicki and Roberts, 1960). Two species of ground squirrels (*Citellus*), whose adrenal weights are known, depart from the usual pattern in rodents and also have significantly larger adrenals in males than in females (Tomich, 1962), but in a third species (McKeever, 1963) the reverse is true. There is little evidence from behavioral observation to show why these conditions may vary so widely among closely related groups or be so similar in distantly related groups of mammals. It seems probable, nevertheless, that carnivores in general are conservative in adrenal responses measureable by the condition of these organs, when compared with the better known lagomorphs or rodents.

#### ACKNOWLEDGMENTS

This research was supported by the State of Hawaii Department of Health and by National Institutes of Health Grant E-2886, Charles M. Wheeler, Principal Investigator. Oliver P. Pearson and Sturgis McKeever read the manuscript and offered many useful suggestions for its improvement. Larry A. Nelson and Albert L. Tester gave their time and advice freely in the more elaborate statistical analyses.

TABLE 2  
ADRENAL SIZE (IN MG/100 G BODY WT) IN THE MONGOOSE BY AGE AND SEX  
DURING A THREE-YEAR PERIOD

CLASS	YEAR	NUMBER	RANGE	MEAN	SE
Young males	1st	34	24.2-58.1	35.8	± 1.44
	2nd	23	21.9-53.8	35.7	± 1.81
	3rd	25	20.6-46.3	32.0	± 1.53
	all	82	20.6-58.1	34.6	± 0.92
Young females	1st	38	26.1-58.7	40.4	± 1.41
	2nd	39	24.4-56.6	39.1	± 1.37
	3rd	56	20.8-60.2	36.3	± 1.24
	all	133	20.8-60.2	38.3	± 0.78
Adult males	1st	71	10.4-72.4	27.4	± 0.92
	2nd	72	11.9-45.0	26.3	± 0.89
	3rd	72	12.8-62.3	25.6	± 0.91
	all	215	10.4-72.4	26.4	± 0.52
Adult females	1st	152	26.2-87.3	52.0	± 1.07
	2nd	84	24.6-97.5	50.5	± 1.68
	3rd	118	26.0-99.6	49.7	± 1.31
	all	354	24.6-99.6	50.9	± 0.73

TABLE 3  
ADRENAL SIZE (IN MG/100 G BODY WT) IN ADULT FEMALE MONGOOSES  
BY REPRODUCTIVE CLASS

CLASS	YEAR	NUMBER	RANGE	MEAN	SE
Active.....	1st	12	41.7-87.3	56.2	± 3.66
	2nd	13	27.6-65.3	43.4	± 2.80
	3rd	11	34.2-68.6	46.5	± 3.20
	all	36	27.6-87.3	48.6	± 2.02
Pregnant.....	1st	42	26.2-79.0	49.9	± 1.96
	2nd	15	25.7-57.7	46.6	± 2.29
	3rd	22	37.9-71.6	53.6	± 2.23
	all	79	25.7-79.0	50.3	± 1.30
Lactating.....	1st	25	45.3-85.0	60.1	± 2.19
	2nd	8	36.6-73.0	53.8	± 4.24
	3rd	7	49.9-62.7	56.9	± 1.68
	all	40	36.6-85.0	58.3	± 1.68
Inactive.....	1st	73	26.7-85.5	49.8	± 1.23
	2nd	48	24.6-97.5	53.2	± 2.58
	3rd	78	26.0-99.6	48.4	± 1.78
	all	199	24.6-99.6	50.1	± 1.04

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# Ecological Studies of Black Coral in Hawaii<sup>1</sup>

RICHARD W. GRIGG<sup>2</sup>

THE BLACK CORALS (Order Antipatharia) are found in all oceans. However, the great majority of the 150 species have been collected with dredges below the limits of human observation (see Table 1). It is therefore not surprising that very little ecological work has been done within this group. The anatomy and taxonomy have been reviewed by Brook, 1889, Cooper, 1907-1909, and Van Pesch, 1914.

In 1958 off Lahaina, Maui, Jack Ackerman and Larry Windley, using SCUBA equipment, accidentally discovered a vast "bed" of black coral in 50 m of water. Previous to this find, the black coral *Antipathes grandis* Verrill had rarely been observed in Hawaii. Only occasionally had divers found stunted colonies in shallow caves where surge was not excessive.

At least three species of black coral are represented in the Hawaiian Islands, all limited to deeper water generally beyond 30 m. Only one species has been recorded in the literature, *A. grandis*, and since it is the most common form, it was selected for this study (Fig. 1).

The purpose of this research was to study and delineate the ecological factors which limit the distribution of this animal to deeper water.

## METHODS AND MATERIALS

### Plan of Work

A series of stations was selected, some with and some without colonies of actively growing *A. grandis* (Fig. 2). Over a period of six months, hydrographic data were collected: light penetration, current, turbidity, surge, oxygen concentration, salinity, temperature, and depth. In addition, the texture and type of substrate were analyzed and population counts were made. By so doing, a comparison between stations could

readily be made and the factors limiting distribution could be outlined.

Branches of the living colonies were transplanted to various habitats, where regular observations could be made to determine if the animal was alive, dying, or dead. These transplants were put in places where it was hoped the effects of environmental extremes could be discovered. For example, the headland off Moku Manu Islands, Oahu, was selected because here wave action and surge reach a maximum, while turbidity, oxygen concentration, salinity, and temperature are relatively constant. On the other hand, the muddy bottom of Kaneohe Bay, Oahu, was also used, for it is extremely turbid, with no excessive fluctuations in salinity, oxygen concentration, temperature, and surge. Thus, it was attempted to measure one factor while keeping the other factors relatively stable, thereby using the environment as a natural laboratory. Experiments in the laboratory were impractical because of the problem involved with handling the animal.

### Collection of Data

LIGHT: Light measurements were carried out with a flat plate irradiance meter which was calibrated with a footcandle meter. Two photoelectric cells were first connected to a galvanometer which was adjusted to a zero reading

TABLE 1

THE BATHYMETRIC DISTRIBUTION OF 66 SPECIES OF ANTIPATHARIA COLLECTED BY THE CHALLENGER EXPEDITION DURING THE YEARS 1872-1876 (BROOK, 1889)

ZONE	METERS	NUMBER OF SPECIES
1 .....	0-18	6
2 .....	18-183	25
3 .....	183-914	26
4 .....	914-1,829	2
5 .....	1,829-3,658	3
6 .....	3,658-5,486	4

<sup>1</sup> Portion of a Master's Thesis, University of Hawaii, completed in July, 1963. Manuscript received December 8, 1963.

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FIG. 1. Large colony of *A. grandis*, at 58 meters, off Lahaina, Maui (Station 9). It is approximately  $3\frac{1}{2}$  meters across and 2 meters high. Photo by Ron Church.

while the two cells were exposed to full sunlight. Then one cell was lowered to the bottom and the difference in electrical potential was measured with the galvanometer. This value can be converted to percent surface light or to  $\text{gm cal. cm}^{-2} (24 \text{ hr})^{-1}$ , and plotted against depth (Fig. 6).

These measurements were taken at an hour when the sun was at maximum altitude on days when turbidity was at a minimum. Thus it was attempted to measure the maximum penetration of light for a particular depth.

**TURBIDITY:** Samples of water were collected from various stations and analyzed with a Tyndall meter so that turbidity values could be compared. Since only relative values were required, it was not necessary to calibrate the Tyndall meter.

**OXYGEN CONCENTRATION:** Dissolved oxygen was measured by the Modified Winkler Method (Hydrographic Office Pub. No. 607).

**SALINITY:** The Knudsen Method was employed to measure chlorinity, which is easily converted to salinity by the formula:  $\text{Salinity} = 0.03 + (1.805 \times \text{chlorinity})$  (Hydrographic Office Pub. No. 607).

**TEMPERATURE:** Temperature as a function of depth was recorded by using a bathythermograph. Data were also collected with a simple  $110^\circ$  Celsius thermometer carried to the bottom by a diver. Temperature increase due to hydrostatic pressure was assumed to be negligible and thus was not taken into account.

**SUBSTRATE:** Portions of the substrate were chiseled with an axe and sledge hammer and

carried to the surface by a diver. The substrate was examined for special features such as texture and chemical composition (e.g.,  $\text{CaCO}_3$  or basalt). It was possible to draw bottom profiles of the substrate *in situ*, using a grease pencil and plastic slate.

**CURRENTS:** Currents were measured in three ways. Data off Sandy Beach, Oahu, and Kaena Point, Oahu, were collected with the aid of the research vessel "Neptune I." In these cases, surface currents were measured by tracking the movement of drifting current crosses.

The Carruthers' Current Cone (Carruthers, 1957) was used when sampling was carried out in an 18-foot skiff. It operates on a water-resistance principle, much like a flag fluttering in the wind. Attached to a stationary line, the cone is lifted by the current at an angle proportional to the intensity of flow. At this point a dissolving cube of sugar triggers the device so that a reading is obtained. Observations of this instrument during use showed that the angle of the cone at any one instant was highly variable, subject to the oscillatory movements of surge

and swell. Hence, under very rough conditions this instrument is not accurate.

The third, and simplest, method of measuring current (and the most accurate) was timing the horizontal drift of suspended particles over a known distance. Currents less than 0.5 knots were referred to as slight, from 0.5 to 1.5 as moderate, and over 1.5 knots as heavy.

**SURGE:** Surge is herein defined as a back-and-forth movement of water over short distances which is generally caused by long waves (swell). It is dependent upon the amplitude and the wavelength of the swell. The period of oscillation usually varies between 6 and 16 seconds. The movement of water particles in waves with short wavelengths is nearly circular at the surface. The radii of these circles decrease exponentially with depth and are imperceptible at a depth which equals the wavelength (Sverdrup, Johnson, and Fleming, 1940). In waves with longer wavelengths, the movement of water particles follows a more elliptical orbit.

When waves begin to "feel" the bottom, the movement of water particles close to the sub-

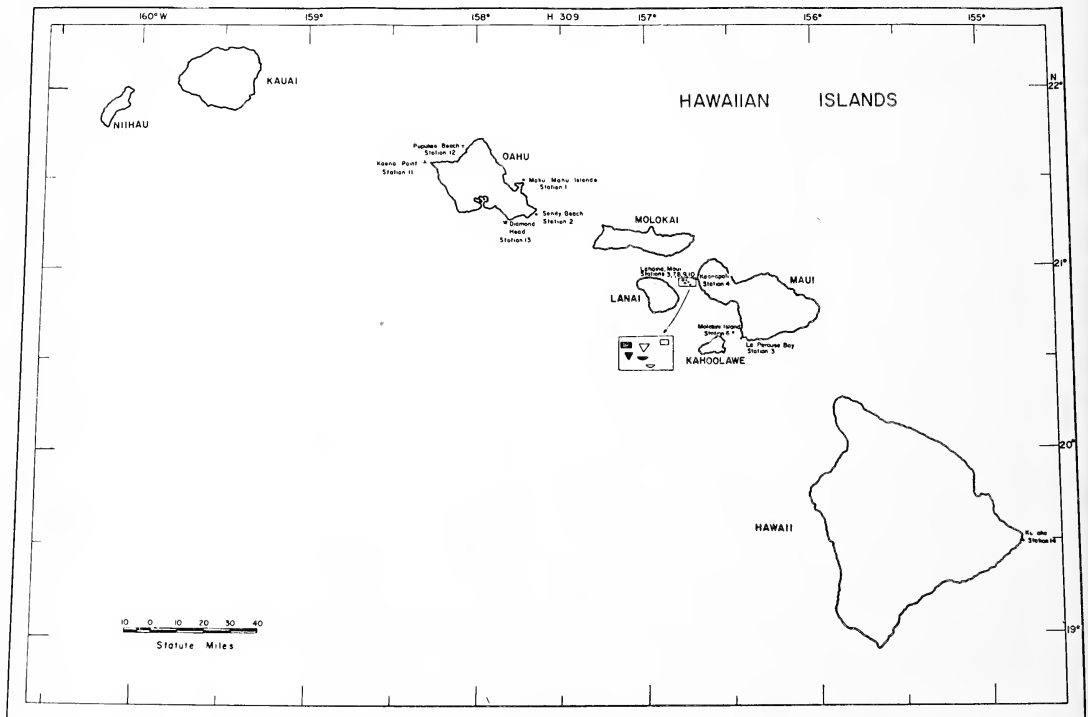


FIG. 2. The position of selected stations in the Hawaiian Islands.



strate will take the form of a flat ellipse so that the water is practically oscillating back and forth in a horizontal plane. This type of surge was found to be of particular importance in this research.

Currents are often superimposed upon surge. For example, if the current is running in the same direction as the swell, it will reinforce surge in one direction and inhibit it in another. If the current is strong enough, the latter direction can be nullified altogether so that motion is uni-directional, speeding up and slowing down depending upon whether current and surge are in or out of phase.

Surge was estimated by watching suspended particles in the water. A back-and-forth movement of water with a horizontal displacement of less than 1 foot was considered slight, of 1–3 feet moderate, and more than 3 feet heavy.

**DEPTH:** Depth was recorded in two ways. A fathometer or continuous depth recorder was used to outline bottom profiles, and a depth gage worn by a diver made *in situ* measurements possible.

**TRANSPLANTS:** Transplanting fixtures had to be made so that broken branches of black coral could be anchored firmly to the bottom. Cement blocks were made with a pipe placed in the center (Fig. 3). A hole near the end of the pipe was threaded so that a bolt could be tightened down on an inserted branch. Metal contact caused the animal to die within 1 cm of the bolt but did not appear to affect the remainder of the branch. The fixtures weighed between 10 and 15 pounds.

In another experiment, a half-inch line was anchored to a projecting piece of fossil coral on the bottom at 43 meters. The end of the line was buoyed up with three metallic floats which at no time were visible from the surface (Fig. 4). Branches of *A. grandis* were tied to this line using a ring-stand clamp and string at 12, 18, 24, and 30 meters.

**POPULATION DENSITY:** Counts of the number of colonies on the bottom were made, using a 10-meter marked line placed on the substrate so that the area could be estimated. Correlation of the population density with the inclination and configuration of the bottom was attempted.

**EPIFLORA AND EPIFAUNA:** Collection of associated organisms was made both at the bottom and on the surface after the colony had been brought up (Fig. 5).

**FEEDING:** Observations on the feeding habits and on the type of food ingested were carried out. In addition a plankton tow was made at 50 meters to determine roughly the type of food present in the natural environment.

## DISCUSSION AND RESULTS

### *Light*

Since colonies of *A. grandis* are found only in deeper waters, where the amount of light is considerably reduced, it seems probable that strong light intensity is important as a limiting factor. Indeed, when colonies of black coral are found in shallow water, their bases are always situated in dimly lit areas such as overhangs and caves. Pérès (1949) has found a similar condition in the underwater "grottos" off Marseilles, where certain deeper sea species were found at much higher levels in submarine caves.

The shallowest depth at which the author has observed *A. grandis* was at 7 meters off Hanauma Bay, where a colony about 30 cm high, was found growing from the ceiling of a very dimly lit cave. Off east Lanai and Hana, Maui, small stunted colonies, which frequently anastomose, are fairly common in caves at about 20 meters. The Kekaha coast of Kauai (off Port Allen) has extensive areas at 30 meters where colonies up to 2 meters high have been taken. It is interesting to note that in all of these regions the water is at times quite turbid because of run-off during heavy rains. Off Lahaina, Maui, where the shallowest colonies are generally found at approximately 40 meters, the water is extremely clear the year round. This area is 5 miles off-shore and thus is not contaminated by run-off water. Light penetration, of course, is affected by depth as well as by the amount of suspended material in the water (Poole, 1938).

These observations suggest that *A. grandis* will settle in water shallower than 40 meters, but only in areas where the light penetration is periodically reduced by the presence of turbid water or by topographical features of the bottom which cut off direct rays of sunlight.

The adult colonies, however, do grow toward the source of light. This fact is especially obvious in caves or under overhangs where in semi-darkness the major branching is always in the direction of the light (Fig. 6).

In addition, adult colonies have been transplanted in calm water as shallow as 1.5 meters

off Coconut Island, Oahu, where they have survived for over 90 days. The light intensity at this point approaches 60%<sup>3</sup> of the surface light. On the other hand, the shallowest colonies of *A. grandis* in the natural habitat do not appear

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<sup>3</sup> Approximately  $475 \text{ gm cal cm}^{-2} \text{ 24 hr}^{-1}$ .

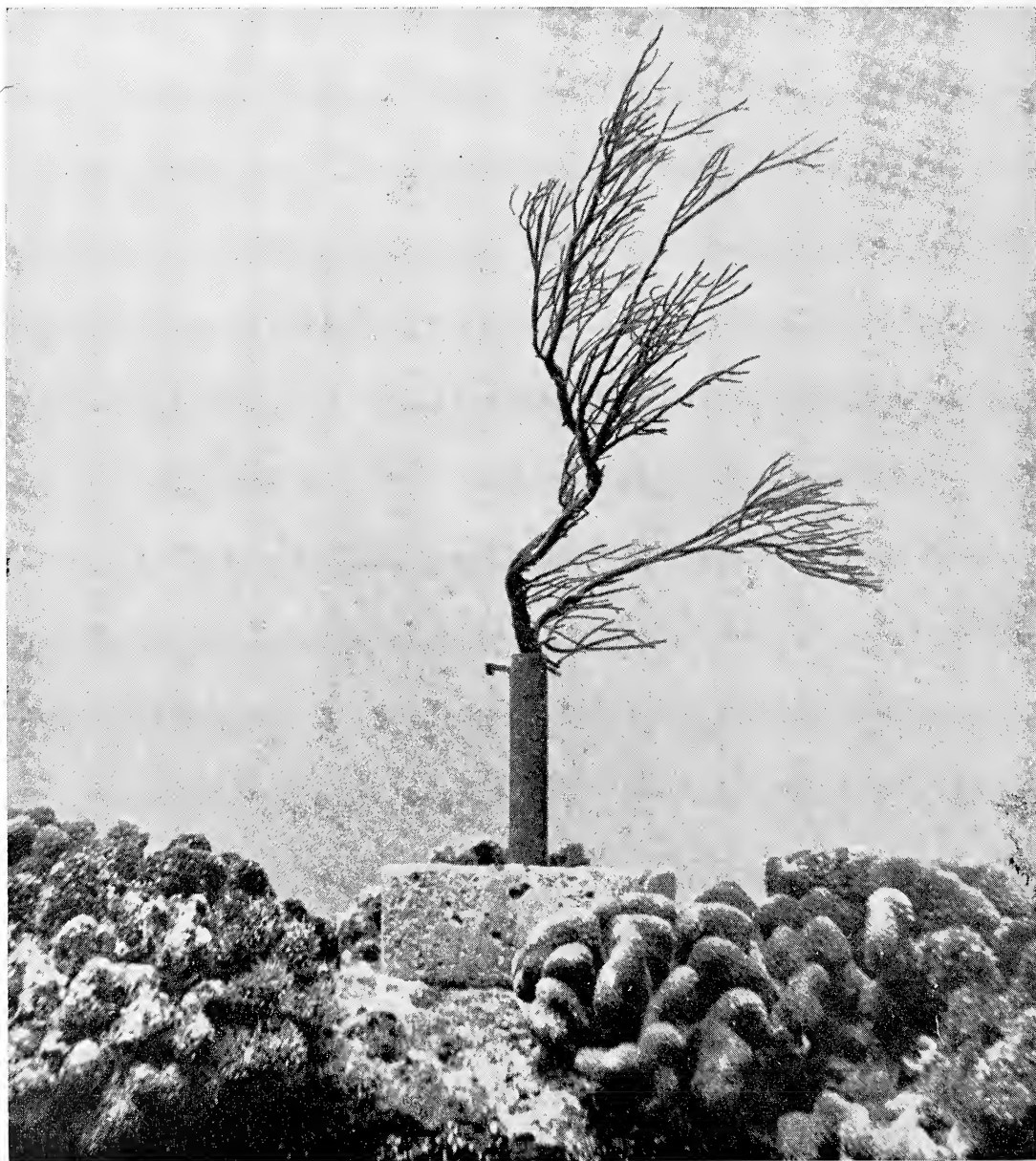


FIG. 3. A living branch of *A. grandis* taken from 43 meters, transplanted in 12 meters of water off Moku Manu Islands, Oahu.

above the 25%<sup>4</sup> level. This value would approximate 35 meters of depth, in the clearest water off the Hawaiian Islands (Fig. 7). Thus, if strong light intensity is a limiting factor, it must be operational only on the larval stage. The larvae, of course, could be limited to deeper water because of other ecological factors.

Nevertheless, in corals that have no photosynthetic algal symbionts light is not essential; and in fact where these corals live within the photic zone they shun direct illumination, living in caves, or on undersurfaces of projecting rocks (Wells, 1957).

Microscopic examination of the tissues of *A. grandis* has not revealed the presence of any zooxanthellae. The planulae, however, have not been observed, and therefore it cannot be said for certain that the larval stage is also free of dinoflagellate symbionts.

*Dendrophyllia*,<sup>5</sup> a deeper water coral that has extended its vertical range into shallow water, has no zooxanthellae and shows no positive reaction to light. Moreover, the planulae settle in darkness, while those of reef builders do not (Edmondson, 1929). Edmondson found that *Dendrophyllia*, like other planulae observed, exhibits a positive phototaxis when first expelled. This response, however, is only temporary, and within a few days the organism moves toward the darker portion of the bottom and either settles or dies. The author suspects that in the case of *A. grandis* larvae a similar mechanism takes place, thereby limiting these animals to the deeper and darker recesses of the reef. This hypothesis is supported by observations in sites shallower than 40 meters, where colonies are found only when the basal attachment is situated in a dimly lit area, such as a cave or an overhang. Beyond 40 meters the population density slowly increases with depth, and at 75 meters the colonies no longer aggregate in shaded areas. Below 75 meters very little observation has been done; only several glimpses by the author have been made in drop-off areas where the population appears to become increasingly dense.

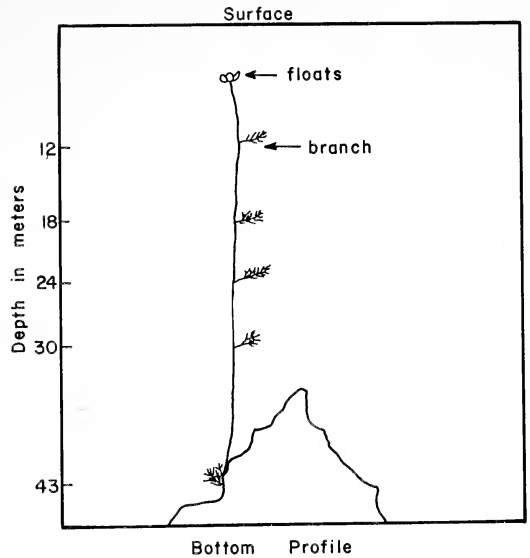


FIG. 4. A line was anchored to the bottom at 43 meters, while the other end was buoyed up by three sub-surface floats. Branches of *A. grandis* were tied at the indicated levels along this line.

#### Transplants and Surge

Colonies of *A. grandis* require a firm substrate so that water movements, current and surge, do not dislodge them. Once dislodged, the colonies are eroded along the bottom and eventually die because of tissue abrasion. Hence, for these studies, it was necessary to improvise anchoring fixtures such that branches could be transplanted from their normal habitat into shallow water (Fig. 3).

Extreme magnitudes of surge were measured at various depths on days when excessively large waves were present. On February 22, 1963, for example, the sea surface was very calm but at the same time a 15-foot swell predominated from the north. In an area with a bottom depth of 40 meters, at slack current, the horizontal movement due to surge at the bottom was 1.5 feet, 3 feet at 20 meters, 6 feet at 10 meters, and 8 feet at the surface. On this day, it was observed that a current of 0.25 knots was superimposed upon the surge at 40 meters, causing water movement to be uni-directional, speeding up and slowing down depending upon whether the current and surge were in or out of phase.

A control was set up by cutting a branch,

<sup>4</sup> Approximately 200 gm cal cm<sup>-2</sup> 24 hr<sup>-1</sup>.

<sup>5</sup> *Dendrophyllia* is said to be incorrectly identified in Hawaii and should be placed within the genus *Tubastrea* (Wainwright, personal communication).



FIG. 5. Large colonies of *A. grandis* must be tied to the anchor line and later hauled to the surface.

bringing it to the surface, and then taking it back to the original site where it was re-anchored to the bottom.

Table 2 summarizes the results of all transplanted branches, including those tied to a buoyed line (transplants 11, 12, 13, and 14). The surge at each station is also included.

The viability of transplanted colonies was determined by observing the polyp condition. Contracted tentacles indicated a less than ideal environment, while mucus formation or denuded portions of the coenosarc indicated that the animal was dying.

The data compiled in Table 2 show that transplanted colonies (numbers 1-7) are able to survive in the calm waters of Kaneohe Bay, Oahu, in quite shallow water for long periods of time. Here the light penetration is very strong, and on clear days approaches 60% of the surface light. Branches transplanted in 12 to 18 meters of water, 50 yards off the wave-beaten head-

land of Moku Manu, did not fare as well, even though the light penetration (40% of the surface light) was less than that in Kaneohe Bay. The lack of marked variation in other chemical and physical factors suggests that surge was the prime factor influencing the survival of these transplanted branches.

The manner in which the animal died also implicates surge and, to a lesser degree, light intensity. Transplants 1, 2, 3, 4, 11, 16, and 18 all illustrate this phenomenon. After approximately one week the coenosarc covering the skeleton of these branches was completely intact, except for a narrow band along the upper surfaces where it was entirely removed. The animal tissues that cover the upper portions of the black skeleton were exposed to turbulent down-eddies accompanying heavy seas. At the same time, the light intensity was strongest upon these surfaces. Hence, an interaction of surge and light intensity acting as limiting factors may be quite possible.

The fact remains, however, that branches did survive in calm water as shallow as 1.2 meters. Hence, surge appears to be the prime factor limiting the viability of adult colonies.

The fact that the tissue was denuded from the skeleton illustrated the abrasive effects of surge. The author believes that suspended particulate material was largely the cause of this abrasion, rather than the frictional drag of the water itself. This view is supported by the fact

that *A. grandis* is able to withstand currents as high as 3 knots in the Auau Channel between Maui and Lanai, where the water is remarkably free of suspended material.

Figures 8 and 9 picture two branches of *A. grandis*, at 12 and 24 meters respectively, which had been secured above the bottom on a buoyed line (Fig. 4), 200 yards off Moku Manu Islands for a period of 90 days. After two weeks about 50% of the branch at 12 meters was alive, while

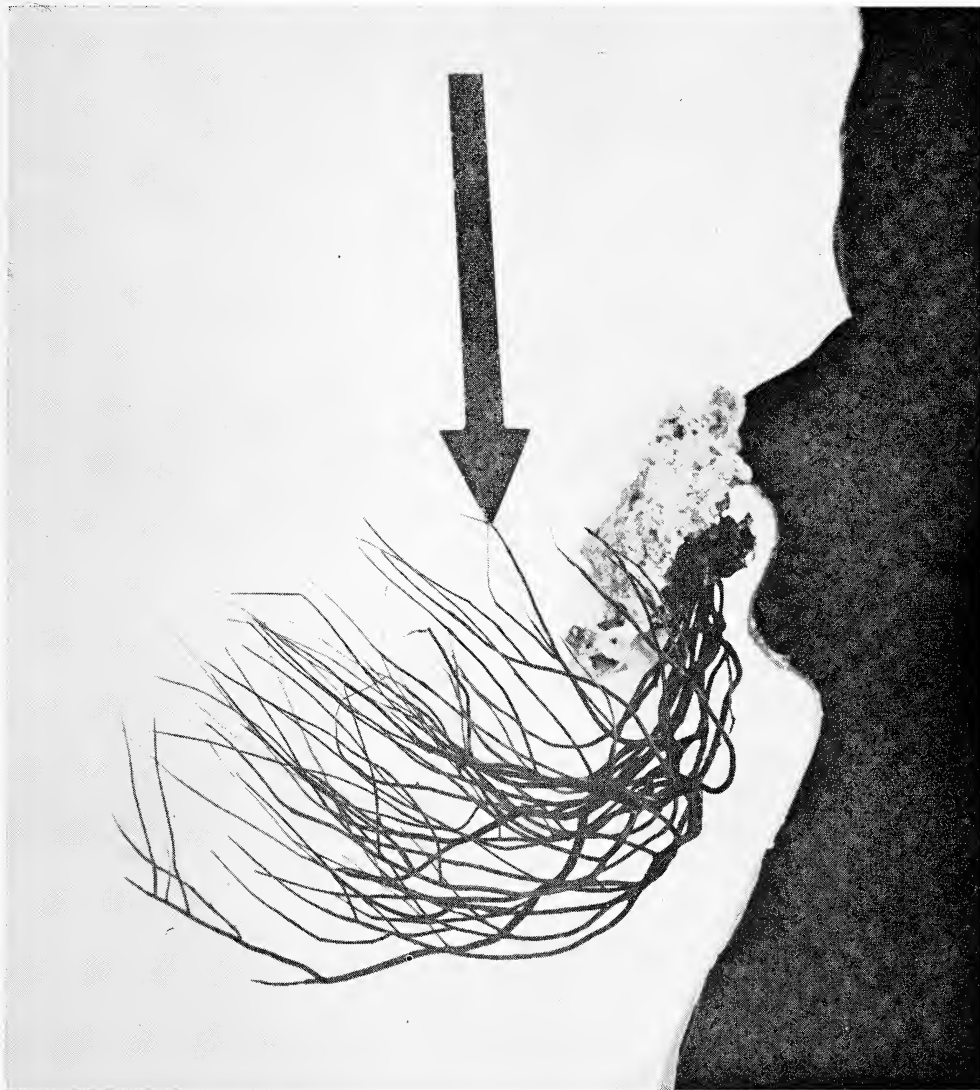


FIG. 6. This schematic photograph simulates the *in situ* orientation to light of a young colony of *A. grandis*, originally collected in 25 meters of water off Kawaiiloa, Oahu. Notice the positive photo-tropism (toward arrow), whereas the site of implantation indicates that the larva is negatively phototactic.  $\frac{1}{3} \times$ .



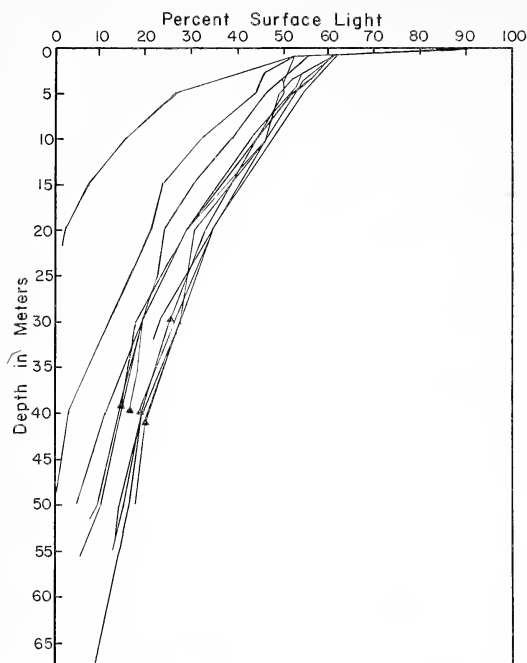


FIG. 7. Percent surface light is plotted against depth. The triangles represent the position of the first colonies of *A. grandis* (shallowest) observed in areas where a shallow bottom rapidly dropped off into deep water.

the entire branch at 24 meters was healthy. After 90 days only 5% of the former branch was alive, while the latter was still completely healthy. The living tissue on the branch in shallow water had been removed by the action of the surge and the denuded skeleton was overgrown with filamentous green algae.

During the 90-day period surge reached excessive magnitudes on three occasions, twice during wind storms with gusts over 70 miles per hour, and once during a 2-day period of 15-foot ground swells. Very turbid water accompanied these extreme conditions.

Transplant 18, which had been fixed on the bottom in 18 meters of water, was 80% alive after the same 90-day period. Along the bottom, of course, there is more particulate material suspended in the water, hence tissue abrasion would be considerably greater than in the case of the branches tied to a buoyed line where the branches were above the bottom.

These results indicate that the limiting effect

of surge is operational to a depth of approximately 20 to 24 meters. Below this level surge will very rarely reach limiting magnitudes. The only specimens of *A. grandis* found in water shallower than 24 meters during this research were in relatively protected areas, where surge was not excessive.

### Turbidity

*A. grandis* is normally found in extremely clear water. Transplanted colonies, however, survived well under varied turbidity conditions. In Kaneohe Bay, for example, where fluctuations of turbidity were quite pronounced, transplanted branches survived for 6 months, after which the experiments were terminated. It does not appear, then, that turbidity per se limits the growth of this animal. If a heavy current or surge, however, is coincidental with very turbid conditions, then the suspended particulate material may become limiting by abrading the tissues of the black coral.

### Oxygen, Salinity, and Temperature

In contrast to inshore areas and surface waters, where fluctuations in oxygen concentration, salinity, and temperature are quite common, the deeper off-shore waters are relatively stable with respect to these factors. At all stations during the period from December through May, the maximum differences in oxygen concentration, salinity, and temperature between the surface and the bottom (60 meters) were only on the order of 2 ml oxygen/liter, 1 ‰ salinity, and 2° Celsius, respectively. The magnitude of these differences is very small, and hence it is not likely that any of these factors is operative in limiting *A. grandis* to its exclusive habitat in deep water.

### Substrate

*A. grandis* requires a firm substrate on which to grow. The type and texture of the substrate is also important in limiting the distribution of this animal. Cary (1914), in his studies on the ecology of gorgonians, observed that distribution was related to the texture of the substratum. He found that, in every case, a one-year-old

TABLE 2  
RESULTS OF TRANSPLANTS

Place		200yd. off Moku Manu Islands, Oahu				50yd. off Moku Manu Islands, Oahu				Control	
Surge		MODERATE to HEAVY		SLIGHT		MODERATE TO OCCASIONALLY HEAVY				Slight	
Depth		12 meters	18 meters	24 meters	30 meters	12 meters	12 meters	15 meters	18 meters	18 meters	43 meters
TIME IN DAYS	1	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive
	3										
	5										
	7										
	14	50% alive	70% alive	100% alive	100% alive	50% alive		70% alive	100% alive	100% alive	100% alive
	21	* During this period two Kona Storms swept this area with winds up to 73 M.P.H.									
	28	50% alive	gone	100% alive	100% alive	20% alive		70% alive	80% alive	100% alive	
	42	10% alive									
	50							50% alive		gone	100% alive
	90	5% alive		100% alive	gone				80% alive		100% alive
	120	Dead									
Number		11	12	13	14	15	16	17	18	19	20

TABLE 2 (Cont.)

Place		Off Coconut Island Reef, Oahu						Off La Perouse Bay, Maui			
Surge		MODERATE				SLIGHT		SLIGHT		MODERATE	
Depth		.6 meters	.6 meters	.6 meters	.9 meters	1.2 meters	1.8 meters	4 meters	1.2 meters	1.8 meters	4 meters
TIME IN DAYS	1	100% alive	100% alive	50% alive	50% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive
	3	100% alive	100% alive								
	5			10% alive	30% alive						
	7			Dead	10% alive				100% alive	100% alive	90% alive
	14										
	21	Dead	Dead		10% alive	100% alive	100% alive				
	28				10% alive						
	42										
	50					100% alive		100% alive			
	90						100% alive	95% alive			
	120							95% alive			
Number		1	2	3	4	5	6	7	8	9	10



specimen had its base in a depression: "Thus the presence of small depressions or cracks where it was least likely for other more rapidly growing organisms to obtain a foothold seemed a prerequisite for fixation."

With *A. grandis* there is similar evidence that a texture preference does exist (Fig. 10). The basaltic ledges, for example, that are found off Molokini at depths in excess of 40 meters, are exceptionally smooth and do not support many colonies. However, where there are depressions, cracks, or other rugged features along these steep facades, one always finds a vigorous growth of black coral.

The type of substrate is also of considerable importance. Few colonies were found growing directly on a basaltic base. On the lava flows off La Perouse Bay, Maui (dated  $1770 \pm 20$  years) and off Kapoho, Hawaii (dated 1926), where several dives were made to 60 meters, not one colony of *A. grandis* was found. Off Molokini, where colonies did attach to a basaltic substrate, there was invariably a thin encrustation of  $\text{CaCO}_3$ . This condition was not apparent unless the colonies were chipped off and brought to the surface, where they were carefully examined.

The most favorable substrate is a fossil coral reef, defined as a  $\text{CaCO}_3$  conglomerate of madre-

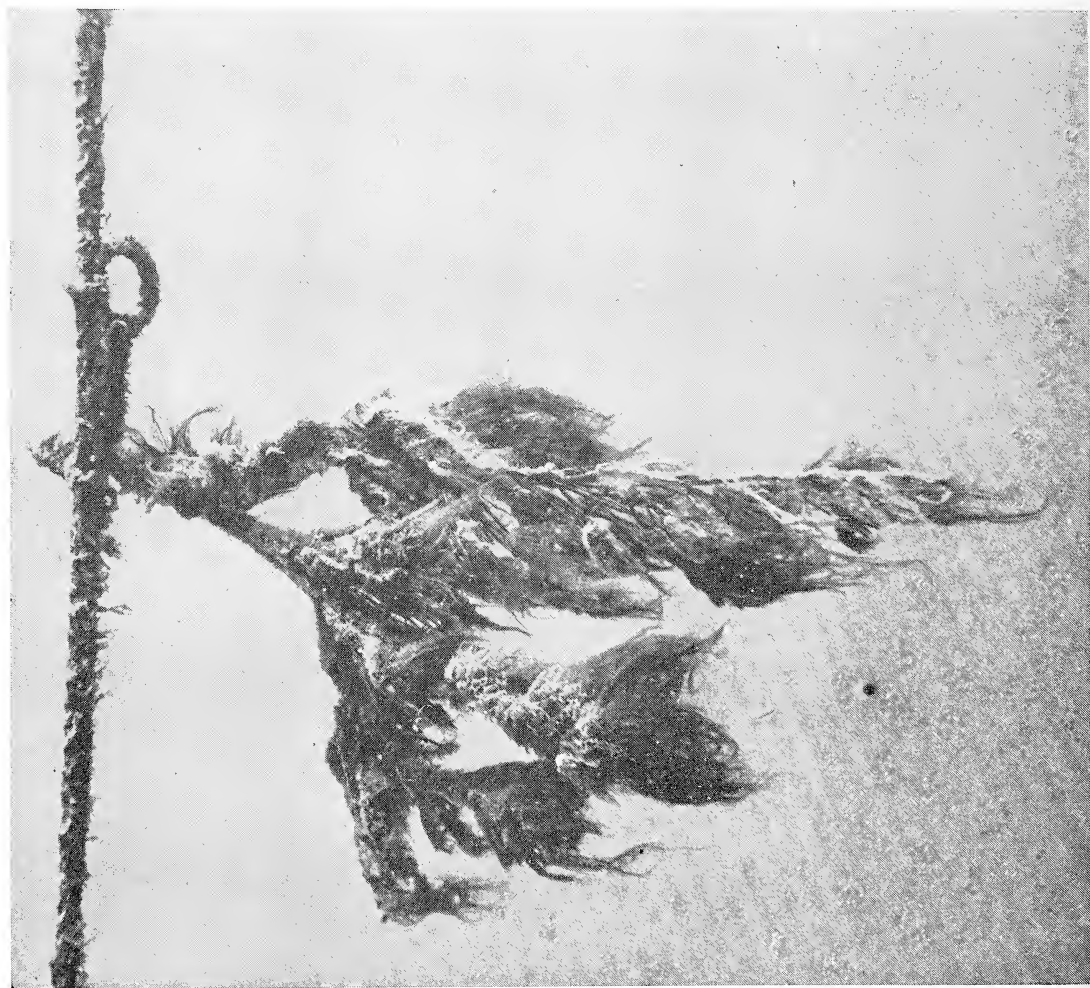


FIG. 8. This branch of *A. grandis* was tied to a vertical line at 12 meters and remained there for 90 days. The animal tissue was completely removed by the abrasive effects of surge, after which the black skeleton was overgrown with filamentous green algae.

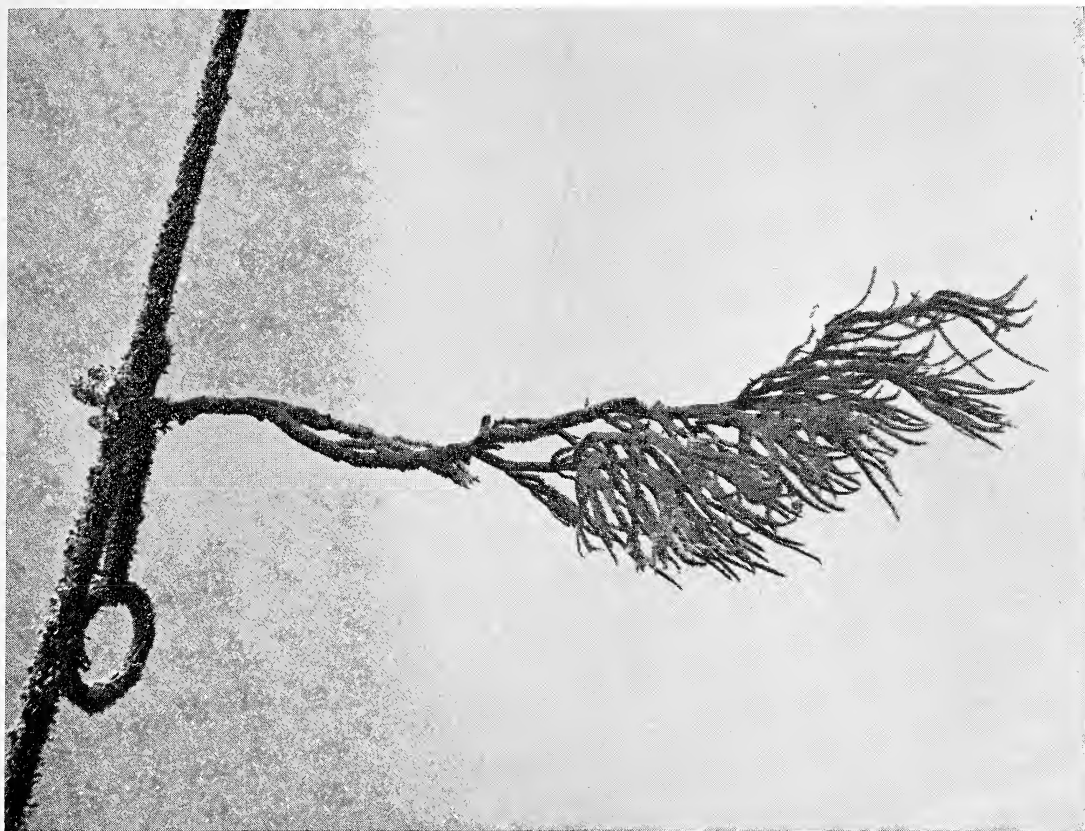


FIG. 9. Tied to a vertical line at 24 meters, this branch of *A. grandis* was quite healthy after 90 days. (Compare with Figure 8, a branch at 12 meters, also fixed to the line for the same 90-day period.)

porian coral cemented massively by coralline algae, Bryozoa, and other calcium-depositing organisms. In Figure 11 the population density is shown in five different areas having a calcium carbonate substrate. The population density off Molokini (a basaltic substrate) ranged between 0.0 and 0.2 colonies/square meter, considerably less than that of a calcium carbonate substrate of equivalent depth and inclination.

The topographical features of the bottom strikingly influence the distribution of *A. grandis* within the zone of observation (75 meters). A sloping substrate, the presence of overhangs, caves, ledges, and drop-offs, all significantly increase the population density. This tendency is illustrated in Figure 11, which shows a high population density in such areas. Below 75 meters this tendency is not so apparent. As was pointed out earlier, the aggregation of *A. grandis* in dimly lit areas is probably a result of a negative

phototaxis of the planulae. A vertical substrate, of course, is relatively free of silt and detrital material which might otherwise inhibit planulae fixation.

In summary, then, the most favorable substrate consists of a rough-textured  $\text{CaCO}_3$  material with many shaded areas resulting from an irregular bottom profile.

#### Current

Food and oxygen come to the sedentary corals by way of water eddies and currents. Such water movements also carry away metabolic wastes.

Hickson (1932) found that a flow of water in one direction over a rocky bottom seems to favor the growth of gorgonian corals. Wells (1957) also pointed out that a current aids the growth of corals: "In still water, accumulation of sedi-



FIG. 10. At 55 meters off Molokini, a 2-meter colony growing on the edge of a jutting ridge of basalt. Notice the barren ledge in the background, which is not supporting a single colony of *A. grandis*.

ment inhibits coral growth, in heavy currents there is too much abrasion by small fragments of coral and rock; coral planulae do not settle or remain attached where currents are strong,

hence moderate currents promote most vigorous growth."

Tide tables (U. S. Coast and Geodetic Survey, 1961) indicate that mixed tides predominate in

Hawaiian waters, with generally one major peak and another lower peak during a lunar day. Tidal elevations vary little from location to location around the islands, and the maximum elevation is only about 3 feet above mean lower low water.

Measurements made during this study illustrate several interesting features of the current. First of all, the surface current and bottom current do not necessarily coincide. They may, in fact, be in opposition during certain tidal moments and wind conditions. The surface currents, of course, are affected by the wind, whereas bottom currents are mainly influenced by tidal conditions and bottom topography.

It was found that the surface currents were swifter than those close to the bottom. This was especially true in areas where the bottom topography was extremely irregular.

Second, along coastal borders and in channel areas, it is known that tidal currents assume the form of a long ellipse (Neumann, 1960). In all cases, except at Kaena Point, Oahu, the currents followed this general pattern, being multi-directional depending upon the tide. It is quite likely that, for this reason, the colonies of *A. grandis* do not orient themselves in one direction with respect to the current.

Off Kaena Point, however, where currents very commonly exceed 2 knots and are in general uni-directional, a definite orientation of the fern type black coral (Genus *Antipathella*) in a fashion perpendicular to the current has been observed. It is significant that specimens of *A. grandis* are absent or extremely rare in this environment. Kaena Point is subject to heavy wave activity in winter months, during which the water is very turbid. This fact, coupled with the intense current, could well be producing an extreme abrasive effect which has been found to be limiting to *A. grandis* (as with the abrasive effects of surge on transplanted colonies off Moku Manu Islands). Evidently the fern type is more tolerant of these conditions.

Third, the current measurements in this study, in all cases except at Kaena Point, ranged between 0 and 2 knots. In shallow water close to shore the currents during any 24-hour cycle re-

main at zero for very short periods, during which time the tide peaks and the current changes direction. Offshore currents are rotary and at no time are completely slack.

Colonies of *A. grandis* do well under these conditions and in fact can tolerate regular currents as high as 2 knots. In those locations where a dense population of *A. grandis* is found (Stations 3, 7, 8, 9), it is significant that the water is free of suspended abrasive particles. For this reason, it is postulated that excessive currents (over 2 knots) may only become inhibiting to the growth of *A. grandis* when the water mass contains a high amount of abrasional fragments such as sand or other particulate inorganic material.

Finally, transplanted colonies in Kaneohe Bay survived very well in areas off Coconut Island where currents rarely exceed 0.5 knot (Avery, Cox, and Laevastu, 1963). These colonies were observed to feed and actually to grow through asexual reproductive processes. It is not known whether sexual reproduction is possible under these conditions, but even if it were the planulae would probably not be able to find a suitable site for fixation.

On the basis of the evidence, then, it does not seem that strong currents are necessary to support the growth of this animal. And since average currents are generally in excess of 0.5 knot in almost all exposed offshore localities in Hawaii, it does not appear that lack of current restricts the growth of *A. grandis*. On the other hand, currents higher than 0.5 knot are necessary to sweep the bottom clean of accumulated sediments. The inclination of the bottom is important, of course, in this respect also. Since colonies of *A. grandis* are found only in cleanly swept areas, it is reasonable to assume that the planulae cannot settle on a substrate covered with an accumulation of sediment.

In summary, then, the most favorable range of average current approximates values between 0.5 and 2 knots. The presence of inorganic particulate material magnifies the abrasive effect of current and therefore lessens the range under which the animal can survive.

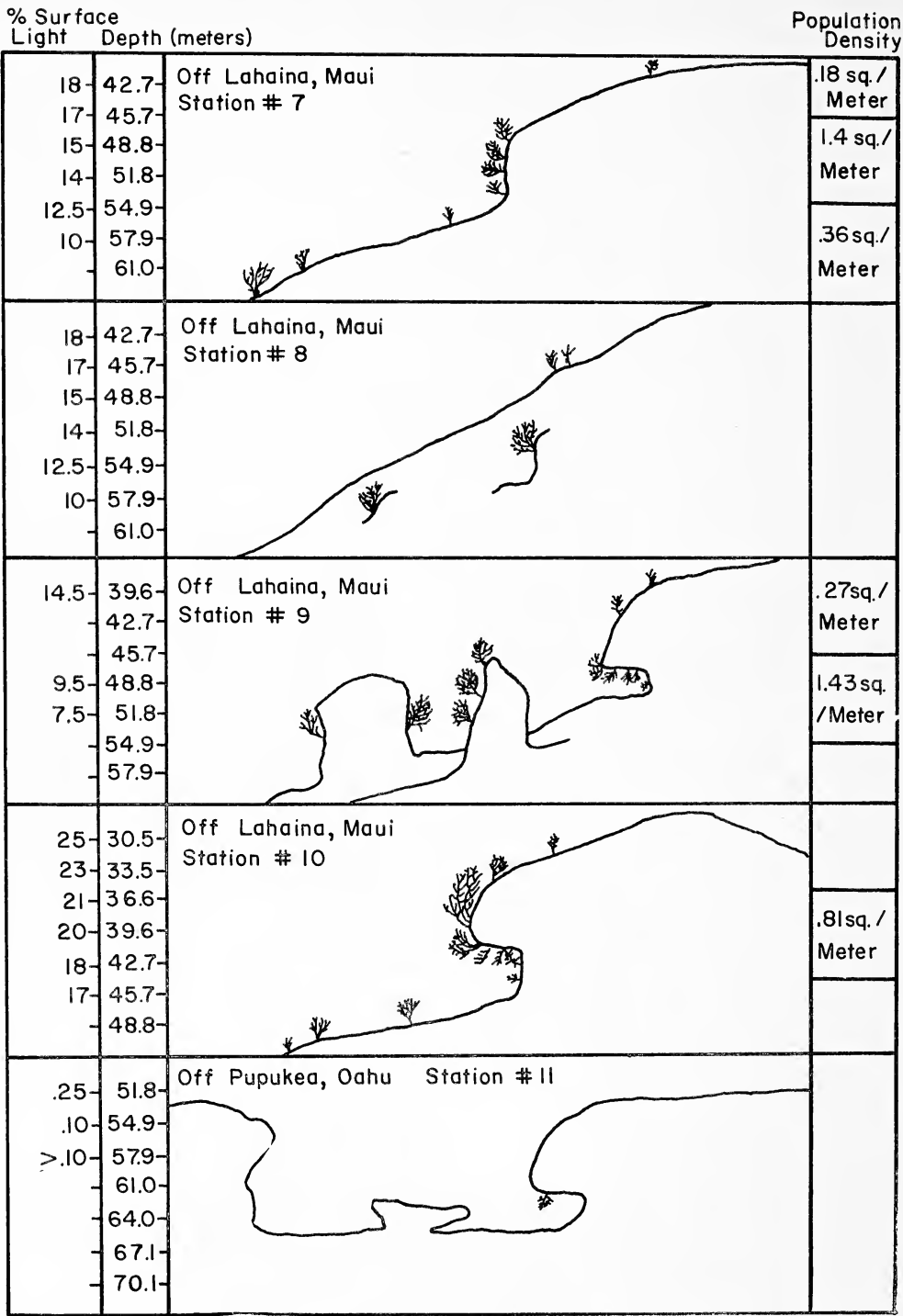


FIG. 11. Bottom profiles of several stations are shown with the depth, light intensity, and the population density indicated.

### Feeding

Edmondson (1929) working on the inshore reef at Waikiki, and Motoda (1939) working in Iwayama Bay, Palau, found a considerable variation in plankton density from day to day. Gardner (1931) found, on the other hand, a small fluctuation in plankton density in his work on atolls in the Pacific.

Wells (1957) states that the food requirements of madreporian corals are low. If this condition holds for the antipatharian corals, then plankton density may not be a limiting factor. This statement is not based on a quantitative study, and is purely speculative.

Plankton-rich water from Kaneohe Bay was introduced into a finger bowl in which living branches of *A. grandis* were observed through a binocular microscope. Ingested plankton, under these conditions, included amphipods, copepods, and chaetognaths (*Sagitta*).

A plankton tow off Moku Manu Islands in 45 meters of water revealed a large amount of detritus, many amphipods, copepods, and foraminifera and, in lesser amounts, radiolaria, dinoflagellates, and ostracods. No chaetognaths were found, hence *Sagitta* may not be a natural food.

Unlike most stony corals, the polyps of *A. grandis* have been observed to be expanded during the day; therefore feeding probably is not restricted to certain hours.

### SUMMARY AND CONCLUSIONS

Ecological factors which limit the distribution of *A. grandis* were studied in an attempt to understand the biology of this species. Research methods are described and ecological and biological information is presented.

The results indicate that:

1. Adult colonies can withstand light intensities up to 60% of the surface incident light.
2. Adults can tolerate ranges in depth (and consequently in pressure) from 1 to 146 meters, indicating that pressure is not likely to be a limiting factor, at least within the littoral zone.
3. Oxygen concentration, salinity, and temperature are relatively stable in the natural environment, and do not appear to be of limiting importance.
4. Adult colonies are limited by the abrasive

effects of surge and cannot tolerate this factor in waters shallower than 24 meters where surge is heavy. In protected areas, however, colonies may survive in very shallow water.

5. Since colonies are commonly found only below 35 meters in most areas in Hawaii, it is postulated that the larval stage reacts negatively to strong light intensities. The lack of marked variations in other environmental gradients supports this view. Evidently the larvae will not settle or survive unless the light penetration is less than 25% of the surface light. In the clearest water around Hawaii this value would correspond to about 35 meters in depth. Only in turbid water or in shaded areas are colonies found any shallower.

6. There is evidence that a  $\text{CaCO}_3$  substrate is more favorable than a basaltic substrate for the growth of *A. grandis*. Also, a rough or uneven substrate will support a larger population than will a smooth substrate. And, finally, within the zone of observation (0 to 75 meters), a vertical and undercut substrate is able to support a denser population than is an otherwise equivalent horizontal substrate. This last phenomenon may be due to the fact that less light is present in such environments.

7. The most favorable range of current for the growth of *A. grandis* is between 0.5 and 2 knots. Presence of suspended sand particles or other particulate material intensifies the abrasive effects of the current, and therefore reduces the range under which the coral can grow.

8. Only animal material was observed to be ingested.

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# Species Composition and Distribution of Pelagic Cephalopods from the Pacific Ocean off Oregon

WILLIAM G. PEARCY<sup>1</sup>

MUCH OF OUR PRESENT KNOWLEDGE about the species composition and distribution of cephalopods of the Pacific Ocean is derived from collections made on cruises of the "Albatross," steamer of the U.S. Fish Commission, during the late nineteenth and early twentieth centuries. "Albatross" collections along the west coast of North America were taken mainly off California and Central America or Alaska, and comparatively few collections were made off Oregon (Townsend, 1901). Neither Berry (1912) nor Hoyle (1904) lists any cephalopods taken off Oregon. A description of a new species of squid (Pearcy and Voss, 1963) and an abstract (Pearcy, 1963) are the only reports of pelagic cephalopods off Oregon.<sup>2</sup> Clearly, more data are needed before comparisons of fauna and generalization on zoogeographic distribution can be made.

## METHODS

A total of 385 collections made between June 1961 and July 1963 with a six-foot Isaacs-Kidd midwater trawl from the "R. V. Acona" provided most of the data on pelagic cephalopods collected off the Oregon coast. Collections were made after dark within the upper 200 m (depth permitting) at a series of stations located 15, 25, 45, and 65 miles, and at another station located between 65 and 165 miles, offshore along parallels of latitude between the Columbia River and the California border (46° 14.4'N, 44° 39.1'N, 43° 20'N, and 43° 00'N). Generally the stations off the central Oregon coast, 44° 39.1'N (off Newport), were sampled every month and other stations bimonthly.

In addition to the 0-200m collections at

various distances from shore, tows were made to provide data on the depth distribution of cephalopods. Over one hundred collections were made to successive depths of 200, 500, and 1000 m over the outer edge of the continental slope at a station 50 miles off Newport. For more details on sampling methods see Pearcy (1964).

Collections were preserved with 10% formalin in sea water. Cephalopods were removed from the collections, identified, and the dorsal mantle length (DML) was recorded.

Occasionally some cephalopods were collected with dip nets under lights at night and some with epibenthic otter trawls.

## RESULTS

The families and species of pelagic cephalopods collected are listed in Table 1. These include 17 species in 12 families. Six species are distributional records for the northeastern Pacific Ocean, reported previously only by Pearcy (1963). They are: *Abraliopsis* sp., *Octopoteuthis sicula*, *Gonatopsis borealis*, *Taonius pavo*, *Cranchia scabra*, and *Vampyroteuthis infernalis*. Only eight of the seventeen species are included in the study by Berry (1912) based mainly on benthic collections.

Although most of these species were collected in the midwater trawl, several were captured by other methods. Two *Moroteuthis robusta* (DML 650 and 1350 mm) were caught in otter trawls off the northern Oregon coast in water deeper than 150 m. This species, reported from California (Smith, 1963) and Alaska (by Dall, in Berry, 1912), was recently reported off Oregon.<sup>2</sup> *Loligo opalescens*, a common inshore myopsid of the west coast of

<sup>1</sup> Department of Oceanography, Oregon State University, Corvallis, Oregon. Manuscript received February 14, 1964.

<sup>2</sup> Added in proof: J. M. Van Hyning and A. R. Magill. 1964. Occurrence of the Giant Squid (*Moroteuthis robusta*) off Oregon. Fish Comm. Oregon Research Briefs 10:67-68.

TABLE 1

LIST OF PELAGIC CEPHALOPODS COLLECTED FROM THE PACIFIC OCEAN  
OFF OREGON, JUNE 1961-JULY 1963

Loliginidae	<i>Loligo opalescens</i> Berry, 1911
Sepiolidae	<i>Rossia pacifica</i> Berry, 1911
Onychoteuthidae	<i>Onychoteuthis banksi</i> (Leach, 1817)
	<i>Moroteuthis robusta</i> (Dall) Verrill, 1876
Enoploteuthidae	<i>Abraliopsis</i> sp.
Veranyidae	<i>Octopoteuthis sicula</i> Ruppell, 1844
Histioteuthidae	<i>Meleagroteuthis holyci</i> Pfeffer, 1900
Gonatidae	<i>Gonatus fabricii</i> (Lichtenstein, 1818)
	<i>G. magister</i> Berry, 1913
	<i>G. anonychus</i> Percy and Voss, 1963
	<i>Gonatopsis borealis</i> Sasaki, 1923
Chiroteuthidae	<i>Chiroteuthis veranyi</i> (Ferussac, 1835)
Cranchiidae	<i>Galiteuthis armata</i> Joubin, 1898
	<i>Taonius pavo</i> Lesueur, 1821
	<i>Cranchia scabra</i> Leach, 1817
Vampyroteuthidae	<i>Vampyroteuthis infernalis</i> Chun, 1903
Octopodidae	
Bolitaenidae	<i>Japetella beathi</i> (Berry, 1911)

TABLE 2

AVERAGE NUMBER OF PELAGIC CEPHALOPODS COLLECTED PER HOUR OF MIDWATER TRAWLING IN TOWS  
TO VARIOUS DEPTHS AT A STATION 50 MILES OFF NEWPORT, OREGON

SPECIES	0-200 M (72 TOWS)	0-500 M (23 TOWS)	0-1000 M (24 TOWS)
(A) <i>Gonatus fabricii</i>	0.5	0.5	0.1
<i>Gonatus</i> spp.	1.2	0.2	0.1
<i>Chiroteuthis veranyi</i>	0.5	0.1	0.1
<i>Abraliopsis</i> sp.	0.7	0.1	0.1
(B) <i>Japetella beathi</i>	0.03	0.21	0.14
<i>Octopoteuthis sicula</i>	0.00	0.04	0.02
<i>Galiteuthis armata</i>	0.00	0.04	0.05
<i>Taonius pavo</i>	0.01	0.14	0.06
	day (9 tows)	night (14 tows)	
(C) <i>Gonatus fabricii</i>	0.2	0.7	0.2
<i>Abraliopsis</i> sp.	0.0	0.7	0.1

North America, was found in several otter trawl collections where the depth was 100 m or less, but was absent from midwater trawl collections. *Rossia pacifica*, another myopsid, was taken mainly in otter trawl collections, as was the large (DML 200 mm) *Gonatus magister*. *Gonatus anonychus* was collected only with a dip net under night lights (Pearcy and Voss, 1963).

The relative abundance of the cephalopods captured by midwater trawling from all stations and depths is shown in Figure 1. *Gonatus fabricii* comprised about 38 percent of the total catch. A group consisting of larval and juvenile individuals of the genus *Gonatus*, but without sufficient differentiation of hooks for specific identification, was next in numerical importance. At least three separate species of *Gonatus* may be represented (Table 1) but, judging from the relative abundance of larger gonatids, most are probably *G. fabricii*.

Geographic Distribution

Little difference in the species composition of cephalopods was noted among the latitudes. *Gonatus fabricii*, *G. spp.*, and *Abraliopsis* dom-

inated the midwater trawl collections at nearly all series of stations. Pelagic cephalopods, as well as mesopelagic fishes (Pearcy, 1964), were rare at the inshore stations off Newport, where the depth of water was 300 m or less.

Depth Distribution

The number of common squid captured per hour of towing appeared greater in tows to 200 m than in deeper tows; this was particularly true of *Gonatus* spp., *Chiroteuthis veranyi*, and *Abraliopsis* sp. (Table 2A). Since an opening and closing device was not used on the trawl, some of the animals found in tows to 500 and 1000 m were probably caught while the trawl sampled through the upper 200 m. Such differences in catches suggest that the four common squids are largely epipelagic in distribution during the night, when most of the 0–200 m collections were made. Comparisons of day and night catches of the two most abundant squids, *G. fabricii* and *Abraliopsis* sp., show that highest catches were made during the night in tows to 200 m depth but during the day in tows to 500 m (Table 2C). This

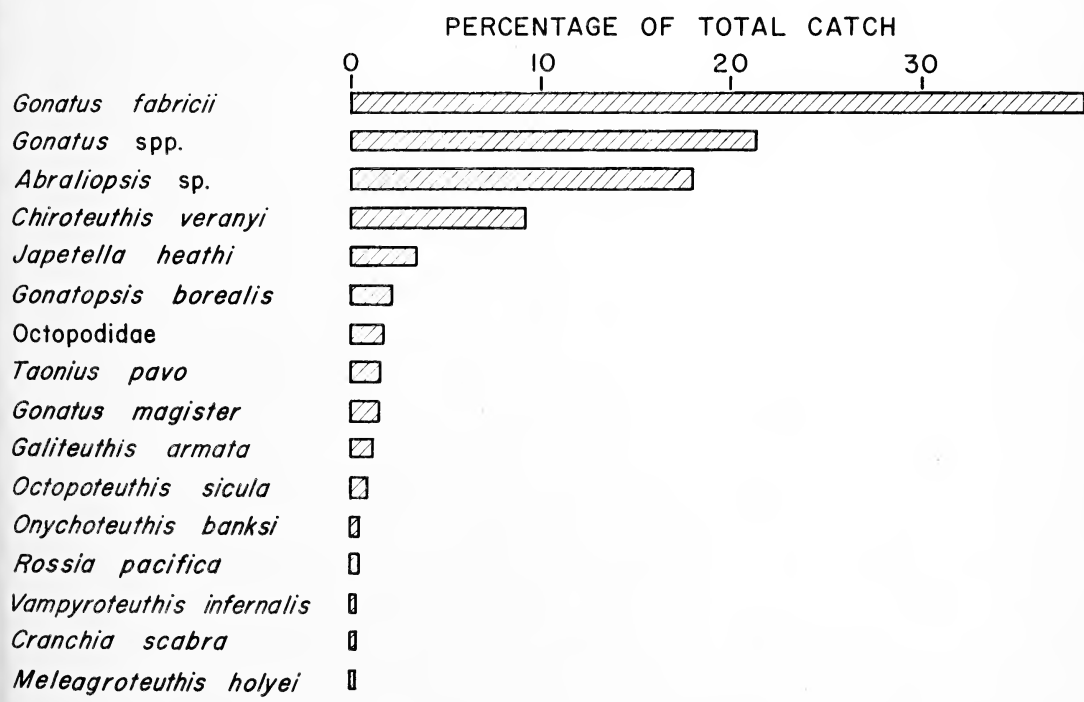


FIG. 1. The relative abundance of pelagic cephalopods found in midwater trawl collections off Oregon.

suggests diurnal vertical migration of these species.

Some of the cephalopods were uncommon in epipelagic waters and are considered to be of basically mesopelagic (200–1000 m) distribution. Four species were more abundant in deep tows than in shallow tows (Table 2B). With the exception of *G. armata*, individuals of these species were occasionally collected in 0–200 m tows after dark at other stations, but they were smaller than those from deeper collections. The bathymetric distribution of *G. armata*, summarized by Sasaki (1929), also suggests that it is a deep water species. *Vampyroteuthis infernalis*, another deep water species, was taken only in tows below 500 m.

Seasonal Variations

Seasonal differences in relative abundance were striking, though species composition apparently was not greatly influenced by season. The number of animals per tow during the summer was about an order of magnitude greater than it was during other months.

TABLE 3

SEASONAL OCCURRENCE OF COMMON  
CEPHALOPODS, 0–200 M COLLECTIONS,  
ALL STATIONS

SPECIES	AVERAGE NUMBER PER TOW	
	JULY–SEPT.	OCT.–JUNE
	(79 TOWS)	(205 TOWS)
<i>Gonatus fabricii</i>	4.9	0.61
<i>Gonatus</i> spp.	1.9	0.32
<i>Chiroteuthis veranyi</i>	0.71	0.20
<i>Abrialiopsis</i> sp.	1.9	0.33

Catches of *G. fabricii* were about eight times higher during the summer, of *Gonatus* spp. and *C. veranyi* about six times higher (Table 3).

Such seasonal differences indicate marked changes in the availability of cephalopods due to changes in susceptibility to capture or to changes in actual abundance. Since the differences could be related to the life history of the

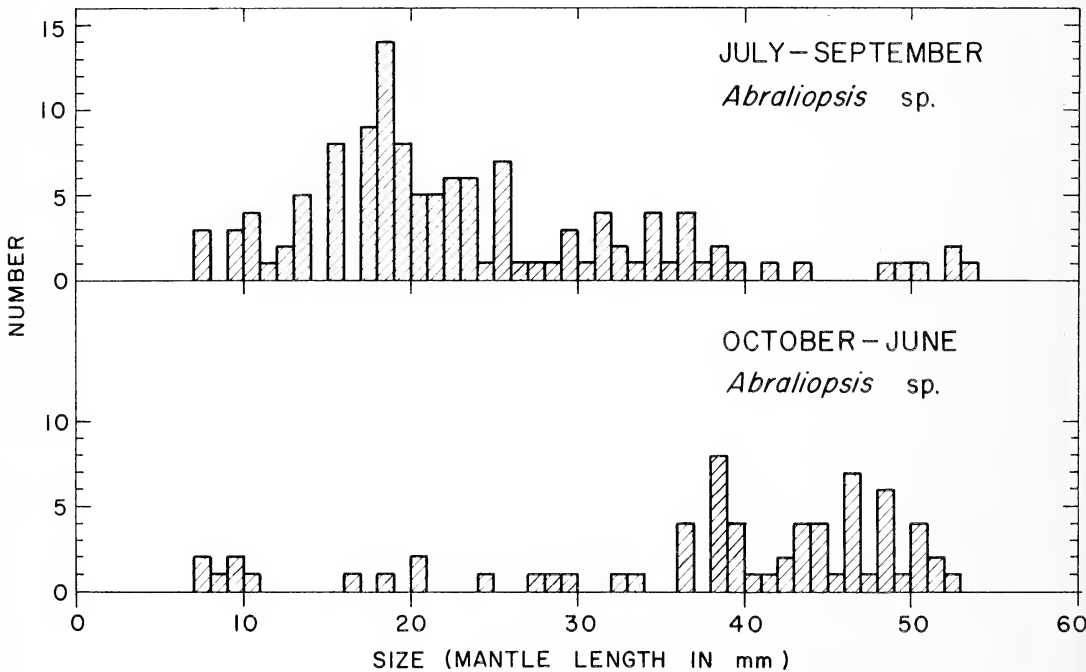


FIG. 2. Size-frequency distributions of *Abrialiopsis* found in midwater trawl samples during the summer (July–September) and other seasons of the year (October–June).

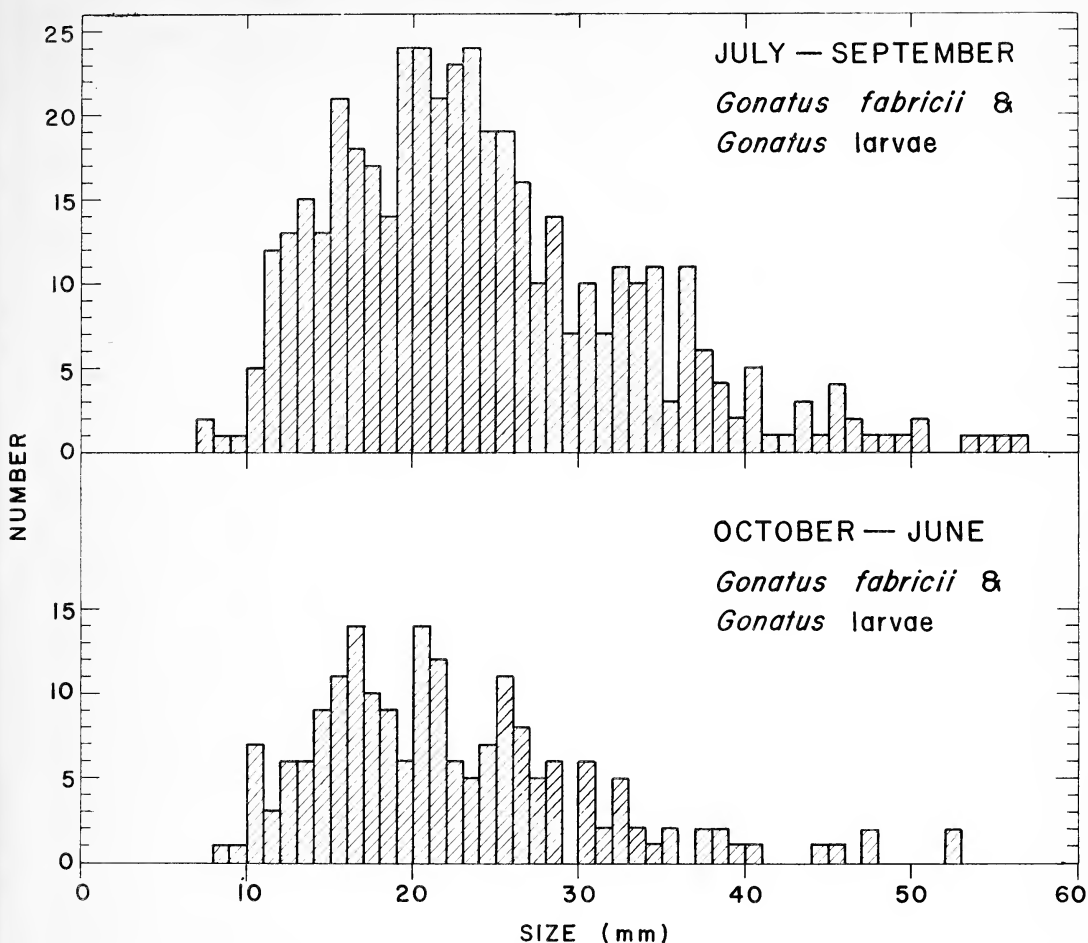


FIG. 3. Size-frequency distribution of *Gonatus fabricii* and *Gonatus* larvae found in midwater trawl samples during the summer (July–September) and other seasons of the year (October–June).

squid in either case, size-frequency distributions were examined.

During the summer the catch of *Abraliopsis* sp. consisted mainly of small individuals (less than 30 mm DML), whereas during other seasons larger squid predominated (Fig. 2). On the other hand, the size distribution of *Gonatus* larvae and *G. fabricii* (assuming they are in fact one species) are similar for both summer and non-summer periods (Fig. 3). This suggests that breeding of *Abraliopsis* is largely seasonal, while that of *Gonatus* is not.

Seasonal differences between the size structures of each species may result from growth, mortality, and movements of the populations.

Growth, and attendant mortality, may explain differences between the size modes and relative abundance of *Abraliopsis* during the two periods. But other factors appear to be involved with *Gonatus*. *Gonatus* specimens over 30 mm in length constituted a larger proportion of the total catch during the summer than in other seasons (21% versus 7%). In addition, the catch of large *Gonatus* per tow during the summer was greater than that of small *Gonatus* (30 mm) during the other seasons. These differences suggest an influx or migration of these squid into slope waters during the summer. Perhaps this is caused by oriented swimming of squids or by a concentrating effect of ocean circulation.

## DISCUSSION

Some squid are notoriously fast swimmers; others are more planktonic than nektonic. Such differences in swimming ability obviously determine the catch composition by any sampling method. Most of the cephalopods collected in the midwater trawl were small. Although a large *Gonatopsis borealis* (DML, 250 mm) was captured, there was evidence that smaller squids than this readily avoid the midwater trawl. For example, *Onychoteuthis banksi* (DML of 100 mm and over) were often observed around night lights, but were rarely if ever captured in midwater trawl collections at the same station and time. The average size of squid was larger in otter trawl than in midwater trawl collections, and, in general, the largest squid were captured in the largest trawls.

Of the identifiable cephalopods found in the stomachs of 66 albacore tuna (*Thunnus alalunga*) collected off Oregon during the summer of 1962, small gonatids predominated. Inasmuch as predators often obtain effective samples of cephalopods (Clarke, 1963), this agreement between the catches of two independent sampling "devices," the midwater trawl and the albacore, was encouraging.

## ACKNOWLEDGMENTS

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## NOTES

### A Gastropod Parasite of Solitary Corals in Hawaii<sup>1</sup>

H. F. BOSCH<sup>2</sup>

OF THE SPECIES of wentletraps (marine gastropods of the family Epitoniidae) that live with or feed upon anthozoan coelenterates, most are associated with sea anemones. Robertson (1963) lists four species of these snails that are known to be either predators or ectoparasites of sea anemones, as well as two others that are assumed to be so. A seventh wentletrap, however, associates itself with a scleractinian, rather than with an actinian. Found attached to solitary corals of the genus *Fungia* in the Philippine Islands (Root, 1958), this wentletrap has been tentatively identified as *Epitonium* aff. *costulatum* by Robertson, who considered it likely that the snail was feeding upon the coral. Thorson (1957) suggested that perhaps all members of the Epitoniidae were adapted for a parasitic mode of life. Evidence supporting both these ideas comes from a similar *Epitonium*-*Fungia* relationship recently noted in Hawaii.

Specimens of the solitary coral, *Fungia scutaria* Lamarck, collected in Kaneohe Bay, Oahu, during the summer and fall of 1963, occasionally had masses of small white eggs attached to them. Usually one or two fragile white snails also clung to the corals or to the egg masses. These snails were identified as *Epitonium ulu* Pilsbry, a wentletrap previously reported only from Hilo, Hawaii (Pilsbry, 1921:376; Edmondson, 1946:138). While only a small percentage of the corals taken in the field had adherent eggs or snails, all corals kept in

aquaria eventually became infested with them during the course of several separate experiments carried out at the Hawaii Marine Laboratory. Thirty *Fungia*, in one instance, became infested within three weeks after having been placed in a large holding tank in order to test their ability to survive in an artificial environment. These corals had been routinely inspected for damages due to collecting prior to being placed in the freshly cleaned tank, and seemed free of *Epitonium* eggs or adults. Yet each coral harbored from one to six snails, with attendant egg masses, at the end of the three week period. The increase in the snail population escaped notice during the interim as neither the snails nor their eggs ever appeared on the upper, feeding surface of the corals. Rather they restricted themselves to the untentacled areas of their host: the periphery or undersurface. By what means the snails were introduced into the tank is not known. Possibly a few eggs had escaped notice when the corals were inspected, or larvae had entered with the sea water when the tank was initially filled. In either instance, it is clear that a number of larvae had rapidly matured and had subsequently produced large clutches of new eggs. Although the sea water in the tank was not filtered or renewed during the three weeks, conditions seemed favorable for larval viability and growth, as many active veligers were prominent whenever egg masses were examined under the microscope. This seemingly rapid development of sexually mature wentletraps, the largest of which attained a length of 16.5 mm, provides an index of maximal growth for *Epitonium ulu*.

Tissue lesions on the undersurfaces of some of the corals (Fig. 1) may have been caused by *Epitonium*, but this was difficult to prove

<sup>1</sup> Contribution No. 221, Hawaii Marine Laboratory. This study was in part supported by a National Science Foundation Summer Fellowship for Graduate Teaching Assistants. Manuscript received May 26, 1964.

<sup>2</sup> Present address: Department of Oceanography, The Johns Hopkins University, Baltimore, Maryland.



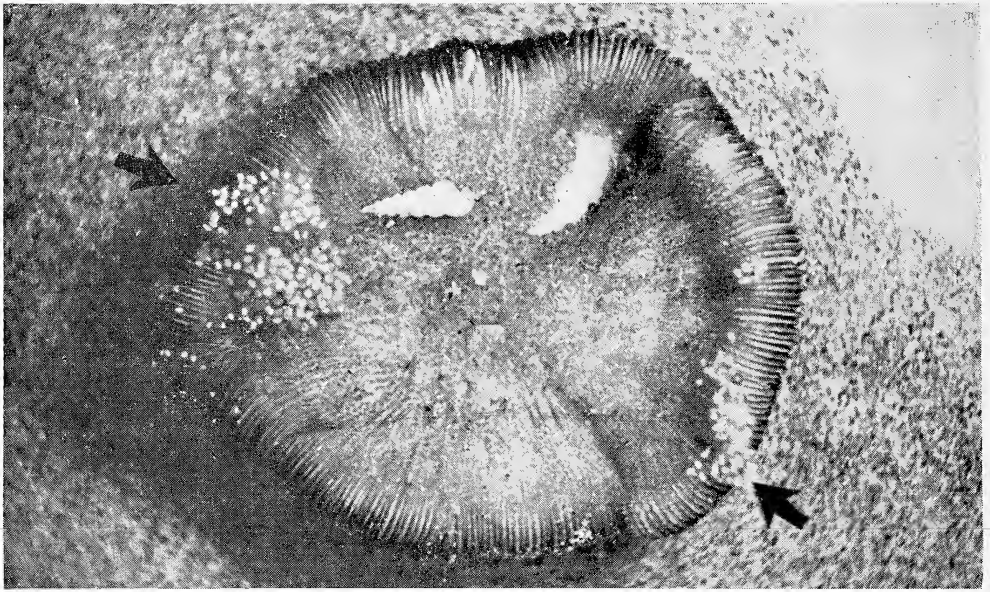


FIG. 1. The undersurface of the solitary coral *Fungia scutaria* Lamarck with the wentletrap *Epitonium ulu* Pilsbry and egg masses (arrows). The wentletrap is 16.5 mm long. White area to the right of the snail is a lesion in the coral's tissue.

inasmuch as the snails avoided the light. While no direct observations of wentletraps feeding on the corals were made, indirect evidence for this behavior was furnished by dissection. Viscera of snails taken from a coral invariably contained copious amounts of pink tissue in which were imbedded symbiotic algal cells (zooxanthellae) and nematocysts, all characteristic of the corals. Moreover, wentletraps placed near corals which had been stained with a vital dye (neutral red) soon became suffused with the same color due to the ingestion of dyed coral tissue. (For such feeding to occur, it was necessary to keep the corals and the snails in the dark.)

Wentletraps in the absence of their egg masses were never found on *Fungia*. Thus the relationship between these two animals may be correlated with the breeding cycle of the snails and may be only intermittent or temporary. The foregoing observations, however, show that *Epitonium ulu* is at least an occasional ectoparasite of *Fungia scutaria*. This evidence supports Thorson's contention that the Epitoniidae in general are adapted to parasitism and also Robertson's view of the parasitic nature of *Epitonium* aff. *costulatum*.

#### ACKNOWLEDGMENTS

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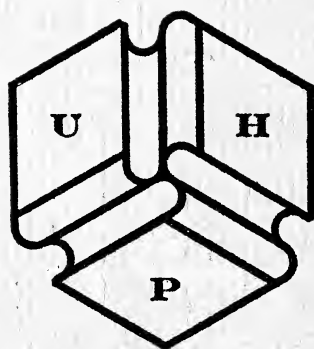
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VOL. XIX

JULY 1965

NO. 3

# PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL  
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

## A SPECIAL ISSUE

*Devoted to Geological, Geochemical, and  
Geophysical Studies upon the Hawaiian Ridge  
and their Relationship to the Proposed Moho Hole*

UCT 6

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## Foreword

GEORGE P. WOOLLARD

THIS ISSUE OF *Pacific Science* is devoted to geological, geochemical, and geophysical studies on and adjacent to the Hawaiian Ridge. It is not only an attempt to summarize in collected form our present state of knowledge concerning Hawaii, its geological environment, and geophysical setting, but is an attempt to establish those deficiencies in knowledge that are pertinent to studies related to the proposed Moho Hole that now is planned to be drilled 125 nautical miles north of the island of Maui. As it is often difficult to assess what specifically should be done in advance of a major operation

such as the Moho Hole, this opportunity to gather together the extensive amount of unpublished studies related to Hawaii having a bearing on the Moho investigation represents a significant contribution to the program.

As a member of the U. S. National Upper Mantle Committee of the Geophysics Research Board of the National Academy of Sciences and as Director of the Hawaii Institute of Geophysics, I would like to express my personal appreciation as well as that of my scientific colleagues to *Pacific Science* for this distinctive contribution to Project Moho Hole.



# Problems of the Upper Mantle and Hawaii as a Site for the Moho Hole<sup>1</sup>

GEORGE P. WOOLLARD

## GEOPHYSICAL DATA PERTAINING TO THE MANTLE

The term "mantle" is a geophysically-derived term believed to have geological significance. As used, it refers to that material lying between the earth's core at a depth of 2900 km, which is also defined geophysically, and that depth at which the velocities of seismic compressional waves increase from values of about 6.5–7.0 km/sec to  $8.15 \pm 0.5$  km/sec. The variations in velocity associated with the mantle are of both a local and regional nature, and in many areas are azimuth dependent. Although the identifying velocity of  $8.15 \pm 0.5$  km/sec may incorporate some bias because of poor measurements, it is significant that out of 316 measurements 223 (71%) lie between 8.0 km/sec and 8.3 km/sec, and that carefully conducted experiments show the same range in values as does the gross sample of data. Anisotropic seismic transmission in the mantle is not uncommon, and can be attributed to selective orientation of the mineral grains. It is not to be confused with boundary slope effects or the effect of progressive changes in heat flow or mantle composition. Regional variations in mantle velocity based on reversed profile recordings are related either to variations in mantle composition or to heat flow. Local variations in velocity may or may not be real and, if real, are probably related to anisotropic transmission. Regional transmission studies such as those based on the GNOME and SALMON underground nuclear explosions, although possibly biased by slope effects due to regional changes in crustal thickness, clearly indicate that the velocity character of the mantle is not uniform beneath the United States, and that the western area has a subnormal mantle velocity probably because of higher heat flow. Similarly, it is found that

certain oceanic areas as the Mid-Atlantic Ridge and the East Pacific Rise have a subnormal mantle velocity which can be correlated with heat flow measurements. That there are true regional differences in mantle composition is suggested by oceanic data. The average mantle velocity found in the Pacific Ocean is significantly greater than that found in the Atlantic Ocean, and also greater than that found on the continents. The respective values are shown in Table 1.

TABLE 1.  
AVERAGE MANTLE VELOCITY  
IN DIFFERENT REGIONS

REGION	MEDIAN (km/sec)	RANGE (km/sec)
Pacific Ocean	8.25	7.65–8.7
Atlantic Ocean	8.10	7.65–8.55
Continents	8.12	7.7 –8.5

It is to be noted that the lower limit of velocity values is much the same in all three areas and is associated in most cases with areas known or suspected of having high heat flow. It is not inconceivable that in these areas there may also be mixing or transformations of crust and mantle material that would also lower the mantle velocity. The high upper limit of 8.7 km/sec observed in the Pacific Ocean is not regarded as significant because it is confined to a single measurement.

That there are variations in mantle material with depth is suggested by seismic refraction measurements, which show in some areas evidence for deep layers below the "M" discontinuity having velocity values in the range 8.5–10.0 km/sec. As this deep structure has been reported in various parts of the world, it is probably real, and in view of the heterogeneous nature of the crust which is well established, it is probable that the mantle is also heterogeneous.

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 85.

That there may be a relation between the composition of the mantle and the overlying crust is suggested by several lines of evidence. For example, the seismic measurements conducted by the Lamont Geological Observatory during the International Geophysical Year over the Scotian Sea show that the mean velocity and thickness of the crustal layer as well as the velocity of the underlying mantle all decrease as the nose of the Scotian arc is approached. If "blanket" data are considered, and all measurements in the Atlantic Ocean area are considered, it is found that there is a positive correlation between the mean velocity of the crust and the mean velocity of the mantle where there are positive isostatic gravity anomalies, and a slight negative correlation where there are negative isostatic anomalies. There is no systematic relationship between the two quantities where isostasy prevails. On the continents the same relations are observed, except that the correlation slopes are much higher and about equal in magnitude in areas of positive and negative isostatic anomalies. In the Pacific Ocean no appreciable difference in relations as a function of gravity is found, and both the negative and positive isostatic gravity anomaly areas show a slight negative dependence of the velocity of the crust on the velocity of the mantle.

These regional differences between the Pacific and Atlantic oceans are also brought out by the relation between crustal thickness and Bouguer and free-air gravity anomalies. Again using "blanket" data, it is found that, for oceanic depths 5.0–6.0 km in both oceans, the anomalies in the Atlantic Ocean are about 20 mgal more negative than in the Pacific Ocean and the crust is about 1 km thinner. As the depth of water is the same, this implies either a difference in mean crustal density or a difference in mantle density, or a combination of the two. As indicated earlier, the median mantle velocity in the Pacific Ocean is significantly higher than in the Atlantic Ocean, which would imply a higher density for the mantle and, hence, greater density contrast with the crust. To maintain the same bottom elevation under hydrostatic equilibrium conditions with a thicker crust, the density of the crust in the

Pacific Ocean must be greater than in the Atlantic Ocean. When one examines mean crustal velocity values, it is found that the values support this hypothesis. This positive correlation between crustal and mantle velocity values strongly suggests that there is a genetic relationship between the crust and mantle. That the mantle and the basal layer of the crust might represent polymorphic phase transformations of the same material, with the depth of the Mohorovicic discontinuity being a function of pressure and temperature relations at depth, has been suggested by Kennedy (1959). Hess (1955) has suggested serpentinization as a reversible process that would also provide a genetic relationship between the crust and mantle.

The most convincing arguments as to the reality of such a phenomenon are the anomalous relations of crustal thickness in areas of crustal subsidence and uplift. For example, the value of crustal thickness determined seismically in Texas, where the crystalline rock basement has been down-warped approximately 7.5 km since late Paleozoic, is about 33 km, which is normal for the surface elevation of 50 m. That the seismic measurement is not substantially in error is indicated by the local gravity anomalies, which show there is essentially complete compensation for the thick column of low density sediments having a theoretical gravity effect of about 80 mgal after allowing for compaction and variations in lithology. As the sediments are either terrestrial in origin or represent shallow water facies, it is probable that the crustal thickness has remained essentially constant, and the progressive down-warpage of the surface has been accompanied by a corresponding upward migration of the mantle at the expense of the basal crustal layer to maintain isostatic equilibrium.

Another line of evidence bearing on this problem is the absence of a pronounced crustal root beneath areas of eustatic uplift. On the Mexican Plateau, for example, the seismic crustal measurement at Durango shows the same sub-sea level elevation for the mantle (–41.2 km) as is found at Calgary, Alberta in front of the Rocky Mountain block. Although Calgary is essentially in isostatic equilibrium,

as is indicated by both gravity data and its crustal thickness of 43 km for a surface elevation of 900 m, Durango has a subnormal gravity field ( $-25$  mgal isostatic anomaly) and subnormal crustal thickness (43.4 km) for its surface elevation of 2200 m. The same anomalous relations are noted in the middle Rocky Mountain region, where the seismic measurement paralleling the Continental Divide actually shows a thinner crust than is found in the adjacent High Plains area of Wyoming. This anomalous change in crustal thickness with surface elevation here is also substantiated by phase velocity dispersion studies of the crust (Meyer, Steinhart, and Woollard, 1958; Ewing and Press, 1959; Steinhart and Meyer, 1961; and Woollard, 1962). As both the plateau of Mexico and the Rocky Mountain area have been subject to eustatic rise since Miocene time, it appears that this uplift has been the result of crustal expansion without any significant deepening of the crust-mantle interface, and without any observable decrease in the velocity of the mantle such as is apparent in the Basin and Range area from regional seismic transmission studies. These relations all suggest reversible exchanges of mantle and crustal material with an appreciable difference in volume and density between the two phases and, as indicated, would explain eustatic uplift and also crustal subsidence such as is noted in the Gulf Coastal Plain without any observable warping of the crust-mantle interface. The tectonic implications of the Kennedy and Hess hypotheses, however, are different. One would have changes in surface load governing the thickness of the crust and the depth to the crust-mantle interface; and the other has movement of surface load responding to changes in surface elevation created by changes in crustal thickness as a result of hydration or dehydration effects at depth.

### *Summary*

The geophysical evidence relating to the mantle can be summarized as follows:

1. The mantle does appear to vary in its physical properties on a regional basis.
2. There is evidence for variations in the

structure and composition of the upper mantle with depth.

3. The mantle in many areas is characterized by anisotropic seismic transmission.

4. The physical properties of the mantle are influenced by anomalous heat flow.

5. There is evidence that the physical properties of the basal layer of the crust are related to those of the underlying mantle.

6. There is evidence that the basal layer of the crust and mantle might represent different phases of the same material which is controlled either by static pressure and temperature conditions at depth or the addition or subtraction of water at depth. Either mechanism could result in an increase or decrease in the volume of crustal material with consequent crustal uplift or subsidence.

7. Gravity data in conjunction with seismic data suggest that isostasy is a real phenomenon for all crustal blocks having a radius of 100 km or more, and that apparent regional departures from isostasy are related to the mean density of the crust rather than to any actual departure from hydrostatic equilibrium between the crust and mantle. The sign of the anomalies appears to be due to the proximity effect, whereby the effect of the near-surface mass distribution predominates over that of the deep-lying mass distribution providing isostatic compensation.

8. A process whereby the crust-mantle interface and changes in surface elevation, mass transfer, and tectonic processes involving changes in crustal mass and volume are automatically accommodated through a reversible crust-mantle transformation would resolve the problem on how isostasy is maintained. Although the resulting mass distribution does not allow for the gravitational effect of sub-mantle variations in mass, the gravity contribution from such deep-seated mass distributions may be nil. As yet there is no evidence that velocity values greater than 8.5 km/sec indicate any increase in density.

### THE MANTLE AS A GEOLOGICAL ENTITY

The geological identification of the mantle is dependent upon laboratory studies of the physical and chemical properties of rocks. Not only

must the rock material chosen satisfy the seismic velocity values noted, but it must also provide a density contrast with the crust that will yield the observed change in crustal thickness with surface elevation and also satisfy the observed change in gravity values with elevation and isostasy.

When one examines the relation between seismic velocity values and density values for different rocks, as determined in the laboratory under surface conditions and high confining pressures, the only rock material that appears to satisfy the above restrictions is a rock composed predominantly of olivine having a density of about 3.33 gm/cc. Eclogites have too high a density and too low a seismic velocity, and no other rock types having the requisite density, such as pyroxenite, appear to have the required high velocity. The companion velocity-density relations for the crust suggest a continental crust having a surficial layer with an observed density of 2.74 gm/cc (from 1158 samples of crystalline rock distributed over North America) and an observed seismic velocity of 5.5 km/sec at the surface increasing to 6.15 km/sec at a depth of 3 km because of the compressibility effect on the modulus of rigidity with no appreciable change in density, and varying linearity through the relations for gabbroic rocks under pressure to mantle relations defined by a velocity of 8.15 km/sec and a density of 3.33 gm/cc which correspond closely to the properties of dunite under high pressure.

This conclusion concerning the mantle agrees with that of Hess (1955, 1962) who, in a recent report (1964) on the serpentinite in the AMSOC core hole in Puerto Rico, concludes that the worldwide similarity of olivines, and of re-constituted serpentines to yield a similar chemical composition, provides a universal rock type that will satisfy not only the requirements of the mantle, but also that of a source rock providing the structure and composition of the oceanic crust. Hess postulates that "layer 2" of the crust is basalt derived by magmatic differentiation from an olivine-rich mantle rock through volcanism, and that "layer 3" is serpentinite formed by the hydration of dunitic mantle material.

There is, however, one problem connected

with Hess' model; namely, how to get the required crustal density stratification and observed seismic structure without having the "layer 2" as full of holes as Swiss cheese. The work of Moore of the U. S. Geological Survey (in press) shows that "fresh" submarine basalts increase in bulk density from 2.2 gm/cc at the surface to 2.9 gm/cc when emplaced under a hydrostatic head of 3000 ft, and that at oceanic depths of 5 km the density is 3.0 gm/cc. This change in density with depth of water is due to the decrease in vesicle porosity with confining pressure. Laboratory studies of the seismic velocities associated with these whole rock basalts likewise indicate an incompatible velocity of about 6.6 km/sec. If the "layer 2" crustal layer is basalt, its low seismic velocity of 4.0-4.5 km/sec would require it to be now mostly serpentine or having a high porosity. The latter could be affected by having it emplaced under subaerial conditions or made up of pillows having sufficient inter-pillow voids to give the required low velocity. Normal basalts having a velocity of about 4.5 km/sec have a density of around 2.35 gm/cc.

The basal crustal layer postulated by Hess to be serpentinite could well exist. Although only one serpentinite tested to date has the requisite velocity of about 6.5 km/sec and density of 2.8 gm/cc under a confining pressure equivalent to about 1.5 kilobars, the fact that such material does occur (Birch, 1964) is sufficient argument to prove that the hypothesis is not an unreasonable one.

Using the velocity-density relations defined earlier (Woollard, 1962), the mean density of the crust on the continents based on seismic measurements is 2.86 gm/cc, giving a density contrast between the crust and mantle of 0.47 gm/cc. In the Pacific Ocean the mean density of the crust is calculated to be 2.90 gm/cc. The Atlantic Ocean crustal data show two groupings, 2.80 gm/cc and 2.90 gm/cc, with an average value similar to that found on the continents.

The fact that these regional differences in derived crustal and mantle density will affect the thickness and depth of the mantle has already been remarked in connection with the difference in crustal thickness observed in the

Pacific and Atlantic oceans for the same abyssal depths of water. Presumably, there will also be a difference in the magmas generated in the two areas and in the types of volcanic material erupted. The data bearing on this point are not too conclusive, as magmatic differentiation with gravity separation of early crystallized heavy mineral constituents such as olivine in the magma chamber can lead to differences in the lavas appearing at the surface. However, this subject will be deferred for the moment, and that of the relation between crustal thickness, surface elevation, the density contrast between the crust and mantle, and gravity relations will be considered.

If the data for seismic determinations of crustal thickness in North America are selected on the basis of areas where the gravity data indicate regional isostatic equilibrium within  $\pm 10$  mgal, and the depth of the Moho is plotted as a function of surface elevation, the following linear relation is found:

$H_c = -(31.7 + 6.0 h) \pm 6$ , where  $H_c$  is the depth of the Moho below sea level in kilometers, and  $h$  is the surface elevation above sea level in kilometers. This formula, however, will not apply to oceanic areas unless the water column is reduced to equivalent crustal material of 2.86 gm/cc density to obtain a synthetic rock surface elevation. That the above formula will satisfy closely observed gravity data can be shown by example.

Under isostatic equilibrium conditions, the free air anomaly in general increases with elevation in accordance with the formula  $F = -3 + 7.5 h$ , where  $h$  is the regional surface elevation in kilometers. This results from the increase in the depth of the compensating mass with elevation and crustal thickness and the integration of the topographic effect from more rugged terrain which increases with elevation. The effect of distant topography and compensation likewise changes with elevation, in accordance with the formula  $C = 13.7 h$ , where  $h$  is the surface elevation in kilometers. The local compensation (crustal root) for an area, therefore, is approximated by the equation:

$$\Delta R = \frac{-BA - F + C}{41.85 \times \Delta \sigma}$$

where  $\Delta R$  is the crustal root in kilometers greater than that at sea level; BA is the Bouguer anomaly mass correction computed using a mean crustal density of 2.86 gm/cc for the crustal section above sea level; F, the free-air anomaly change with elevation; C, the effect of distant topography and compensation; and  $\Delta \sigma = 0.475$  gm/cc to obtain agreement with the free board to root ratio of 1:6, as determined empirically.

For an assumed surface elevation of 2000 m, the Bouguer anomaly mass correction is (BA)  $= 2 \times 41.85 \times 2.86 = 239$  mgal. The free-air effect (F)  $= -3 + 7.5 \times 2 = 12$  mgal. The distant compensation effect (C)  $= 13.7 \times 2 = 27$  mgal.

$$\therefore \Delta R = \frac{-239 - 12 + 27}{41.85 \times .475} = \frac{-224}{19.87} = 11.3 \text{ km}$$

On the basis of elevation alone,  $\Delta R = 6.0 h$ , where  $h$  is the surface elevation in kilometers. For  $h = 2000$  m,  $\Delta R = 6.0 \times 2 = 12.0$  km.

The agreement is excellent, considering the approximate nature of the equations defining the free-air effect and that for distant topography and compensation; the uncertainty in defining the empirical relation between crustal thickness and elevation, and the unknown contribution of structure in the upper mantle. A crust having a density of 2.86 gm/cc with a mantle having a density of about 3.33 gm/cc, as derived from seismic velocity-density relations, reasonably satisfies both isostasy and known gravity relations to elevation. It constitutes a major argument for the mantle's having a composition comparable to that of dunite.

Let us now turn our attention to the geologic evidence offered by volcanic eruptives. It has been known for some time that the basaltic lavas forming the Hawaiian Islands differ from those of most other oceanic islands in that they are predominantly tholeiitic with a very low percentage of potassium. It has also been established that the alkalic basalts, trachytes, and andesites found in Hawaii are late stage eruptives, and probably are differentiates of what was originally tholeiitic basaltic magma. The predominant alkalic basalts found in the Society Islands, Samoa, Fiji, and other islands pre-

sumably could also represent magmatic differentiates of an original tholeiitic magma. Alternate explanations are: (a) there are regional variations in the chemical composition of the mantle, (b) the composition of basalt is a function of partial melting of the mantle, or (c) of the depth at which the magma is generated. In connection with this hypothesis, the laboratory investigations of Yoder and Tilley (1962) suggest that the composition of the magma can be a function of pressure and temperature, and that alkalic basalt represents a deeper, higher pressure environment than does tholeiitic basalt.

To investigate this problem the writer and Gordon A. Macdonald started a program of integrated geophysical and geological studies in the Hawaiian Islands and Samoa in 1963 under the sponsorship of the National Science Foundation. Although this study has not been completed, preliminary results which will be presented in this report suggest that magmatic differentiation best explains the relations noted in Hawaii and probably Samoa also. On other islands, such as the Line Islands group, gravity data suggest that the primary magma extruded was alkalic, but there is no clue as to the depth of origin. The only actual data bearing on this point are the relations noted in Japan by Kuno (1959), who found that the alkalic basalts are associated with zones of deep-focus earthquakes and the tholeiitic basalts with shallow-focus earthquakes. If there is a relation between earthquake focal depths and magma generation, and there does appear to be such a relation in Hawaii with magma supplying present active vents originating from about 60 km, Kuno's observations and the Hawaiian data both appear to support the findings of Yoder and Tilley. With regard to partial melting Engel and Engel (1964), in an excellent review study of oceanic basalts, note that this implies a mantle that is even more deficient in radiogenic elements than is tholeiitic basalt. These investigators, on the basis of their comprehensive study of basalts in all oceanic areas, conclude that deep-lying oceanic basalts in general are tholeiitic; that they are all remarkably similar in composition; and that, since their volume is about a thousand times greater than that of alkalic basalts, the

alkalic basalts are probably magmatic differentiates of tholeiitic magma.

Thus, the geologic evidence for the composition of the mantle from studies of basalts is not conclusive, and even may be said to be contradictory. The writer's approach to the problem has been through geophysical studies. As tholeiitic basalt has a higher density than alkalic basalt, there should be a real difference in the gravity field associated with primary volcanic pipes supplying the different lavas. On the assumption that these pipes were filled with essentially undifferentiated mantle material in the early stages of intrusion, when the bulk of the lavas was being rapidly extruded and the bulk of the volcanic pile was being developed, as noted recently off Iceland, and that these pipes were sealed off at the top soon after the external pressure was sufficient to develop intermittent volcanism with subsequent eruption via flank rifts developed by doming and fracturing of the volcanic pile or through secondary vents, the primary pipes should contain a substantial sample of the primary magma with little or no differentiation at shallow depth. Certainly the field relations and geophysical measurements on Oahu suggest such a history. On the island of Oahu the two primary pipes whose caldera lie on opposite sides of the island at or close to sea level are marked by local gravity anomalies of about  $+110$  mgal ( $+310$  mgal absolute Bouguer). Later vents, such as Koko Head and Diamond Head, have no appreciable gravity effect, although the bulk density of the surface flow material is only  $2.3$  gm/cc. The rift flows forming the Koolau Mountains, representing an intermediate stage in the volcanic history of the island, are marked by intermediate gravity anomaly values of about  $+50$  mgal. Somewhat similar conditions are noted on the island of Hawaii, where there is still active volcanism. All of the primary pipes, such as Mauna Kea, Mauna Loa, Kohala, Hualalai, and the present active pipe at Kilauea, are marked by local gravity highs of about  $+100$  mgal. All stages of eruptive history are represented. Mauna Kea is dormant; Mauna Loa, the principal source of lava in the recent past, erupts only periodically and mostly through flank fissures; and Kilauea represents an active,

intermittent volcanic caldera. Seismic earthquake focal depths suggest that Kilauea draws its magma from a depth of about 60 km and, as with all other major Hawaiian volcanoes, the late stage lava is now alkalic.

The high gravity anomalies reported by Strange, Machesky, Woollard (p. 350, this issue) for Oahu and by Strange et al. (p. 381, this issue) for the Hawaiian Islands, as a whole, can only be explained by high density rock material having a density of about 3.1 gm/cc coming essentially up to the surface. Seismic refraction measurements in the old Koolau caldera near the town of Kailua on Oahu (Adams and Furumoto, p. 296 in this issue) show that here there is material with a seismic velocity of about 7.0 to 7.6 km/sec at a depth of about 4000–6000 ft. This is similar to the velocity of 7.6 km/sec observed for what may be the mantle at a depth of 6 km on a seismic refraction line along the north shore of Oahu paralleling the Koolau Mountain Rift zone. In addition, deep reflections from about 12,000 ft were obtained on the west side of the Koolau caldera which could represent an inter-crustal magma chamber. On another seismic-refraction line paralleling the south shore of Oahu, the mantle has a velocity of about 9.0 km/sec at a depth of about 23 km. Thus, there is good evidence for mantle-like material at shallow depth in the old Koolau pipe on Oahu. However, this pipe, as well as all others (Malahoff and Woollard, in a forthcoming issue of *Pacific Science*), is characterized by marked local magnetic anomalies, and there is a problem as to the nature of the pipe material. Certainly one would not expect dunite.

In Samoa the gravity measurements likewise show a local gravity high of the same magnitude and absolute value (+300 mgal Bouguer) over the site of the ancient caldera defined geologically, with little gravity effect over the later volcanic pipes. These data, therefore, suggest that the alkalic basalts present are the results of magmatic differentiation, and that they constitute a superficial cover over earlier tholeiitic basalt.

Gravity observations on the Line Islands, however, do not bear out the above relations.

The local anomaly values show no pipe effect and have absolute Bouguer values of less than +200 mgal. This is true on Washington, Christmas, Palmyra, and Fanning islands. Johnston Island, which lies on the extension of the Line Island Ridge, however, does have values that get up to about +270 mgal absolute Bouguer. The relations along the Line Island Ridge, therefore, are variable, and either reflect a difference in pipe material, or extreme variability in the degree of differentiation that has taken place in the pipe, or else marked differences in the size of the pipes or depth of the primary material. To some extent similar results are found in the Hawaiian Islands, as on Niihau there is no pronounced pipe effect, and the Bouguer anomalies do not exceed 290 mgal.

In this connection, it is of interest that the gravity values on Bermuda, while showing a smaller local anomaly than on Hawaii (+80 mgal), are higher on an absolute scale (+355 mgal Bouguer) (Woollard, 1954).

By way of contrast with these results, gravity studies of calderas of andesitic volcanoes in Japan all show the pipe area to be defined by a pronounced gravity minimum of 25–30 mgal. A similar relation is observed over granite intrusions on the continents, and the recent report on the AMSOC hole in Puerto Rico (Bromery and Griscom, 1964) shows a local minimum of 20 mgal over a serpentinite body that was once a high density peridotite. Hess (1964) feels that the magma in the latter case originated within the mantle rather than in the crust. Granite presumably originated within the crust during mountain orogeny. Andesitic magmas possibly could be generated in the mantle, as suggested by laboratory studies, but as yet there are no corroborating data other than earthquake foci relations.

### Summary

The geologic data taken in conjunction with physical and geophysical data indicate the following:

1. The mantle, in general, appears to be similar to dunite, with seismic velocity of 8.15 km/sec and a density of 3.33 gm/cc.
2. The mean density contrast of the mantle and crust is 0.475 gm/cc, giving a free board



to root ratio of 1:6 for conditions of hydrostatic equilibrium.

3. The changes in crustal root for changes in surface elevation based on the above ratio can be reconciled closely with gravity data for changes in surface elevation, assuming isostatic conditions.

4. Tholeiitic basalts appear to be derived directly from mantle material which rises with possible differentiation but little change in physical properties to within a few thousand feet of the surface in primary volcanic pipes on many oceanic islands.

5. Tholeiitic basalts predominate over alkalic basalts by a factor of 1000:1.

6. The volcanic history of the Hawaiian Islands suggests a progressive differentiation of flow material from tholeiitic basalt to trachyte and andesite with time.

7. Mantle-like material is trapped at shallow depth in all primary pipes along the Hawaiian Swell and also in Samoa.

8. Presumably the mineralogy of this trapped mantle-like material is not the same as that existing in the mantle, since it recrystallized under low pressure and temperature conditions and lost certain constituents through eruption and gaseous dissemination into the surrounding rocks.

9. All oceanic islands do not appear to be characterized by tholeiitic basalts, and there is no evidence on many islands for primary pipes containing mantle-like material; the pipes have either a lower density rock filling, or there is no density contrast with the surrounding flow material.

10. A firm case cannot be made for variations in mantle material from geologic data, although geophysical data suggest that such is the case.

11. A dunitic mantle could provide an adequate source material for the oceanic crust if the basaltic upper layer either has a porosity of about 21% or contains abundant glass.

#### HAWAII AS A SITE FOR THE MOHO HOLE

Arguments for drilling to the Moho are many, and range from determining whether it is similar to chondritic meteorites to obtaining

a better understanding of the isostatic mechanism. It is not germane to the present report to review these arguments or to discuss their validity. Our purpose is to review the scientific arguments for locating this operation in the Hawaiian area rather than elsewhere. It goes without saying that practical considerations, such as the depth of crust to be drilled, the depth of water, distance from a supply base, logistic support, local weather and sea conditions, labor supply, and other factors affecting costs, and the chances of a successful operation will play a role in deciding the drilling site. Even if all these factors were not equal between two potential sites, there would be other factors of a scientific nature that might well justify the selection of one site over another. The writer believes that these additional scientific benefits in the Hawaiian area make it the logical site for the proposed hole to the mantle. Some of these have been touched on in the previous discussion. However, before taking these up, the practical considerations will be reviewed briefly.

#### *Depth of the mantle*

The seismic crustal measurements in the vicinity of Hawaii by Shor and Pollard (1964) show that about 125 miles north of Maui the mantle has a subnormal depth of about 9 km below sea level. This is about 4 km less than the normal depth of about 13 km encountered in the Pacific Ocean for the depth of water (2380 fm), and 3 km less than that commonly encountered in the Atlantic Ocean. As this depth to the mantle has been verified by subsequent seismic refraction measurements made by Western Geophysical Company, it is probably realistic. The question naturally arises as to why the mantle should lie at a subnormal depth here and whether there is some associated factor that will mitigate against normal mantle material being present. From Figure 1, which shows the bathymetry in the area, it is seen that the NSF-recommended site (marked by a cross) lies on the south slope of the Hawaiian Arch and about 50 miles north of the buried extension of the Molokai Fracture zone near where it disappears beneath the North Hawaiian Trench. There is nothing in the bathymetry, therefore,

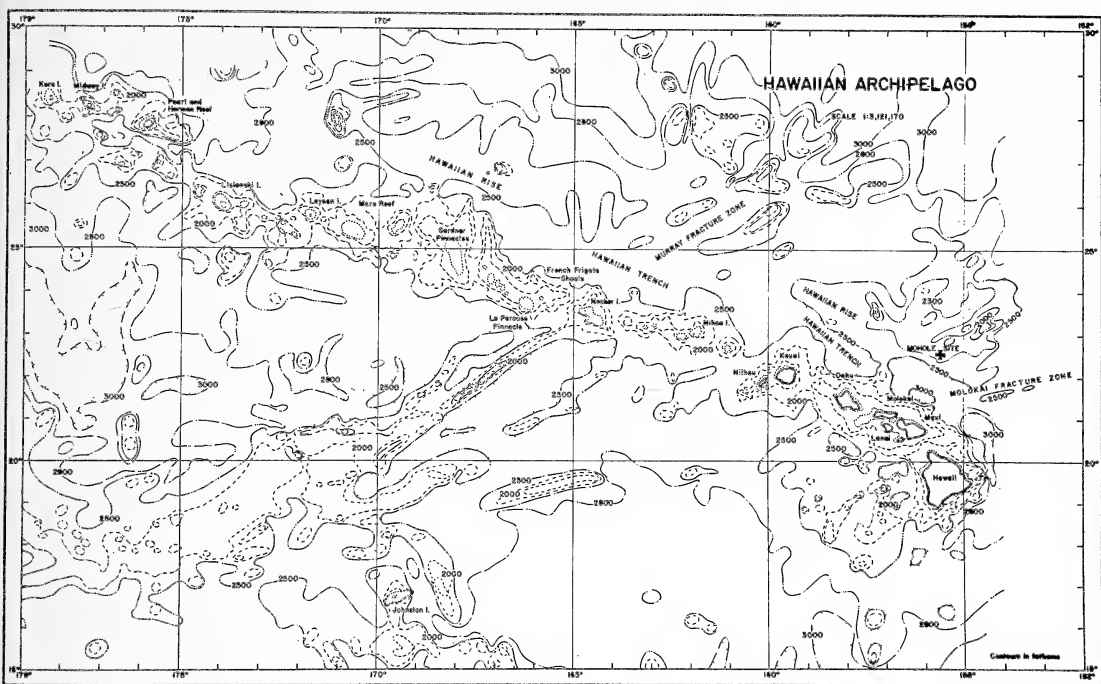


FIG. 1. Bathymetric map of the Hawaiian Archipelago, showing proposed Moho Hole site (cross). Contour intervals in 100 fm.

that suggests abnormal conditions at depth. Similarly, when the gravity (Fig. 3 in Strange et al., p. 386 in this issue) and the magnetic (Fig. 2) data are examined, no subsurface abnormalities such as a buried volcanic pipe or crustal faulting are suggested. The shallow depth of the Moho, on the basis of the seismic measurements, results from up-warping of the crust in response to crustal subsidence beneath the Hawaiian Ridge.

#### *Depth of water*

The depth of water at the recommended site as indicated is approximately 2380 fm (4350 m). Ship positioning, therefore, probably will have to be maintained acoustically through signals from on-bottom "pingers."

#### *Depth of drilling required*

The total depth of drilling required below the sea bottom to reach the mantle, according to the analysis made by NSF of the seismic

data, is about 4.6 km, of which about 0.3 km is sediment.

#### *Weather conditions*

The area is remarkably free of storms, bad weather, and temperature extremes. The temperature ranges, in general, between 70° and 85°. The prevailing trade winds blow at 12–20 mph from the east much of the year and seldom exceed 30 mph. Because of the constancy in wind direction, a surface current set to the northwest of about 1.0 knot can be expected. Storms, when they do occur, are usually from the south. In these cases, seas will not be high because of the sheltering effect of Maui and resulting short fetch. Average swell runs about 6 ft, and storm waves about 25 ft. Although tsunami waves are to be expected, in the open sea these waves are hardly perceptible and probably no greater than the diurnal tidal change of 1–2 ft.

#### *Seismicity*

There is no record of earthquakes in the

vicinity of the proposed drilling site. Nearly all the local earthquakes occur along the Hawaiian Ridge and mostly on the island of Hawaii. The magnitude of these earthquakes seldom exceeds IV, and the nearest recorded epicenter to the proposed drilling site lies 120 miles to the south of it.

#### *Auxiliary location control*

Both air and sea location systems (Omni, LORAN C, tracking radars) exist in the Hawaiian Islands, which will be of great value in establishing the site location and in maintaining navigational control between the drilling site and shore base once operations are started.

#### *Stability of the water column*

Inasmuch as bottom pingers will probably be used to hold positions, variability in mean acoustic velocity presumably could pose a problem. However, maximum annual variation in mean acoustic velocity between the surface and bottom is only about 0.85 ft/sec (approximately 1 part in 5000). Differences in position control due to seasonal changes in water column structure and temperature, therefore, should not exceed 1 m.

#### *Distance from supply base*

The recommended site is about 125 miles from Kahului airport on the island of Maui, which is a practical range for helicopter support.

#### *Base support*

Land support facilities on Maui include docks, an airport, warehouse and housing facilities, and four daily commercial flights to and from Honolulu, and once-a-week freight barge service.

#### *Labor supply*

There is a plentiful local supply of semi-skilled and skilled labor in Hawaii. Wages are the same as those prevailing on the mainland West Coast.

#### *Cost of living*

Living costs are somewhat higher than on the mainland because most staple food stocks and fuel have to be imported. Rents are also

higher because of higher building material costs. However, these cost increases are offset in part by the fact that neither home heating nor air conditioning is required. The net increase in living costs over those on the mainland is within 5%, which is no greater than the difference noted between mainland cities, and less than between some cities.

#### *Scientific cooperation*

The Institute of Geophysics at the University of Hawaii at Honolulu has staff, equipment, a research vessel, shops, and an IBM 7040 and 1410 computer that can contribute to the success of the operation. The university also has an engineering school and departments in all the basic sciences, and graduate programs and staff in meteorology, geophysics, geochemistry, geology, astrophysics, oceanography, hydrology, and geodesy. The staff and facilities of the U.S. Geological Survey at the Hawaiian Volcano Observatory, as well as the U.S. Coast and Geodetic Survey Geophysics Observatory staff can also be called upon for cooperative assistance.

#### *Other facilities*

There are many facilities that can contribute directly or indirectly to the program. The U.S. Navy, for example, maintains a major shipyard and repair facility at Pearl Harbor. Honolulu is the primary mid-Pacific operations base for the U.S. Coast Guard. Emergency helicopter support is available from both the Coast Guard and the U.S. Marines. Honolulu is served by several steamship lines, and three scheduled airlines maintain service to the mainland with over 12 flights in each direction every day. Honolulu is a major manufacturers' distribution center, with parts and service facilities covering a broad spectrum of industrial equipment. There are commercial shipyards and shops, and one of the world's major heavy construction firms has its main office in Honolulu, as does the company that calibrates and maintains most of the Navy's electronic equipment.

#### *Official support of local government*

The state of Hawaii has a science-conscious Governor and Legislature, who can be counted

on to provide not only moral support but also possibly some financial aid for support facilities and any legal assistance or legislative action required to facilitate the operation.

*Scientific benefits to be obtained*

The principal scientific advantages in drilling the Moho Hole in the Hawaiian area are briefly as follows:

1. The mean mantle velocity in the area north of Maui ( $8.27 \pm .2$  km/sec) is normal for the Pacific Ocean, and agrees closely with the mean of all measurements in the Pacific ( $8.25$  km/sec). The mantle rock sampled, therefore, can be expected to be representative for the Pacific area as a whole.

2. The mantle material, on the basis of the seismic velocity measurements in the proposed site area, is truly anisotropic in that the spreads oriented north to south show a velocity of approximately  $8.0 \pm 0.1$  km/sec, whereas those oriented east to west show a velocity of  $8.55 \pm .2$  km/sec. Cores here, therefore, should permit the determination of the cause of anisotropic transmission and identify the minerals causing it.

3. The crustal structure at the NSF-recommended site shows not only a local thinning of the crust, but also a somewhat subnormal thickness of the basal crustal layer, which has a higher than normal velocity ( $6.96$  km/sec) as compared to  $6.84$  km/sec for the area as a whole. In addition, the overlying intermediate crustal layer has a somewhat greater than normal thickness and lower than normal velocity of about  $5.8$  km/sec. It appears, therefore, that this thickening of the second crustal layer has been made at the expense of the underlying basal layer. There also may have been attrition of the basal layer from below, as evidenced by the rise in the crust-mantle interface. The alternate interpretation for the rise in the M discontinuity is that it is caused by domal uplift due to outward flow of mantle material from beneath the Hawaiian Ridge caused by crustal subsidence. The upper crustal layer having a velocity of about  $4.2$  km/sec is normal for the area with a thickness of about  $1$  km.

As the crustal structure is not strictly normal, one might argue that this is not the

place to drill to the mantle. Conversely, one can also argue that it is the place to drill in that a significant physical-chemical process involving both the mantle and crust and two seismic discontinuities appears to be active and can be studied here. If Hess is right, and serpentinization of olivine-rich mantle rock determines the location of the Moho; and if the crust is really serpentinite, as Hess postulates, with a thin veneer of extruded basalt on top, here is an opportunity to study an area where serpentinization appears to be migrating as a wave front through the crust, with a following wave front of deserpentinization. Whatever the mechanism that will explain the observed structure, it appears to be of fundamental importance and one that might well have a bearing on the whole problem of the development of crustal structure, the thickness of the crust, the depth of the Moho, and how isostasy is maintained. A drill hole here, therefore, would provide auxiliary scientific information of considerable importance.

4. Auxiliary considerations are:

a. The U.S. Geological Survey and the University of Hawaii are conducting continuing and extensive petrological, geochemical, and geophysical studies in the present active volcano at Kilauea, which is drawing material from a depth of  $40$ – $45$  km below the mantle-crust boundary. Thus, there will be a continuing scientific program related to the Moho Hole operation.

b. The Hawaiian primary lavas are tholeiitic and, because of their depth of origin, can be related directly to the composition of the underlying mantle. Knowing the chemical composition and mineralogy of the mantle, the process of differentiation leading to tholeiitic and alkalic basalts can be realistically studied.

c. The high velocity, high density pipe filling on Oahu, at a depth of less than  $6000$  ft, can be drilled at relatively low expense to determine the chemical and petrologic nature of recrystallized mantle material which appears to have undergone very little change in physical properties, but which may represent an important phase in the chain of transformations from mantle material to tholeiitic basalt.

d. The existing wealth of geophysical, geo-

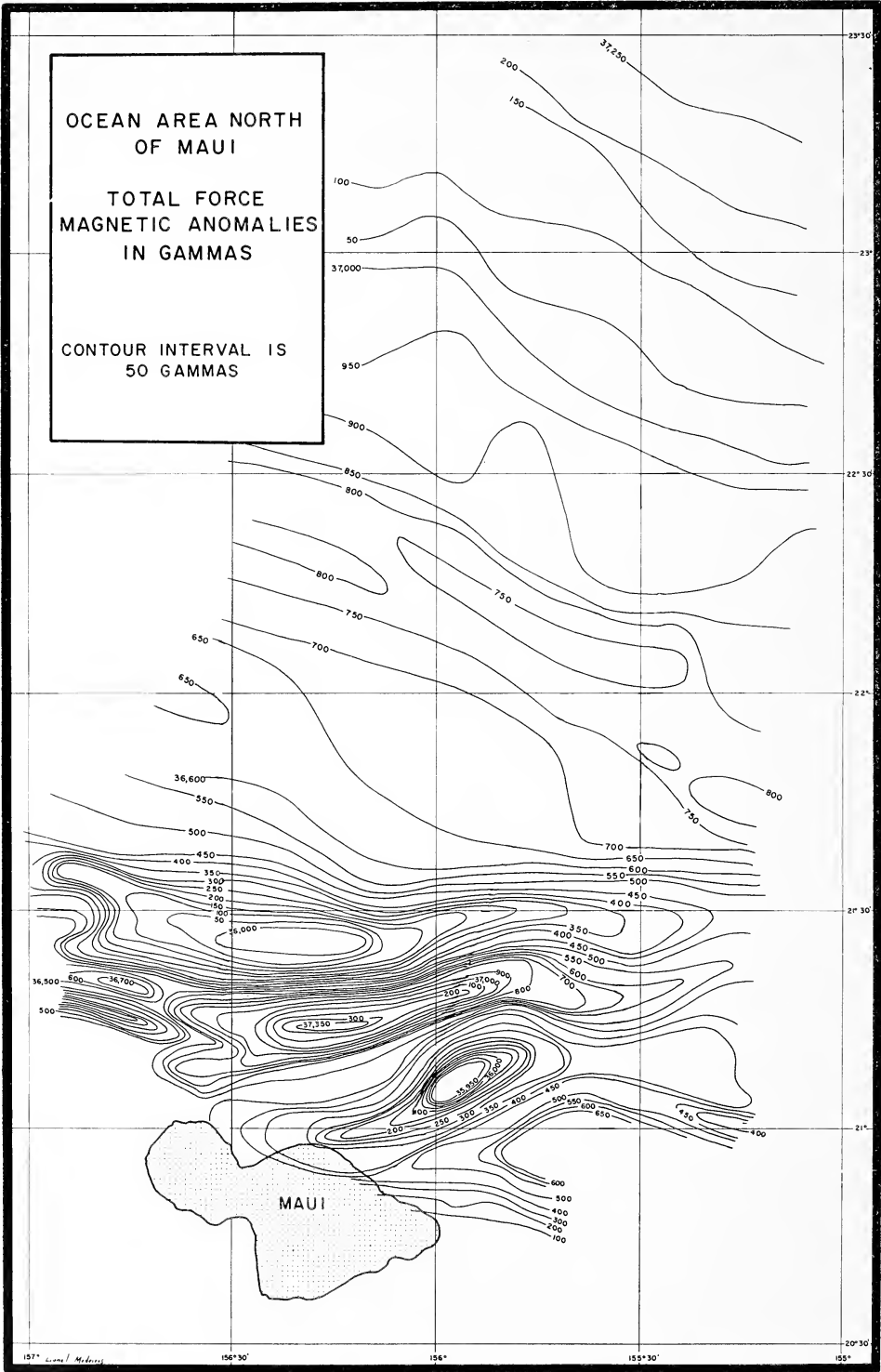


FIG. 2. Map of total force magnetic field north of Maui.

chemical, and geologic information in the Hawaiian area will permit a more intelligent analysis of the Moho Hole data than can be undertaken in almost any other area.

### Summary

The arguments for locating the Moho Hole at Hawaii are all favorable from the practical viewpoint of bringing off a successful operation. This is extremely important from the standpoint of obtaining support for drilling other such holes elsewhere. Failure to drill to completion—because of some natural catastrophe, such as a hurricane; the incurrence of higher than anticipated costs because of logistic support problems over distances greater than that associated with the Hawaii site; delays caused by inferior local support—might well jeopardize future operations of this type. It is imperative, therefore, that the initial undertaking be made where possible adverse extraneous factors affecting the operation are minimized. Admittedly, the depth of drilling to the Moho off Hawaii is somewhat greater than that determined off Antigua, but a technology capable of drilling to 8 km should be capable of drilling to 9 km equally as well. The difference in dollar costs is not regarded as significant, because the additional drilling costs off Hawaii will be offset by savings in logistic and supply costs.

From a scientific standpoint, there is no question regarding the superiority of Hawaii as a site for the Moho Hole. There are no indications of faulting or other tectonic factors that might influence pressure and temperature relations, and hence, the character of the mantle. Although the structure of the crust at the recommended site is locally somewhat abnormal, this actually is a favorable circumstance in that drilling here would permit a second major scientific problem, the origin of the crust, to be investigated in an area where it is undergoing change. A third major scientific problem, the derivation of tholeiitic basalts, probably can be resolved by drilling off Hawaii. The drilling of a shallow hole to sample mantle-like material on Oahu would further add to the significance of the program and give valuable information on the chemical homogeneity of the mantle over a span of some 200 miles. Finally, the results

can be integrated with those of related geological, geochemical, and geophysical research programs that have been operating in Hawaii for a number of years, and which will be maintained on a continuing and expanded basis, and thus contribute to the significance of the operation for many years to come.

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# The Lithologic Constitution of the Crust and Mantle in the Hawaiian Area<sup>1</sup>

GORDON A. MACDONALD

NEARLY NOTHING IS KNOWN by direct observation about the composition of either the mantle or the crust below sea level in the Hawaiian region. Almost the only information about either comes from the interpretation of geophysical studies.

We generally refer to the crust beneath the Pacific basin as basaltic but, with the exception of a few samples dredged from widely separated localities (Engel and Engel, 1964), which are indeed basaltic, all we really know about the sub-Pacific crust is the velocity of seismic waves in it.

Above sea level the Hawaiian mountains consist largely of tholeiitic basalt, with a minor cap of alkalic basalt and related rocks ranging from ankaramite to trachyte, and an even smaller volume of nephelinites and related rocks. Below sea level the rock constitution is known only by implication and from a few samples dredged from very limited areas. Evidence suggests considerable isostatic sinking of the older of the Hawaiian Islands, and it may be presumed that the rocks down to as much as 3,000 ft below sea level in the older islands are the same as those we see above sea level in the younger volcanoes. Other than that, tholeiitic basalts have been found by dredging along the east rift zones of Kilauea and Mauna Kea volcanoes and the south rift zone of Mauna Loa, down to a depth of 12,000 ft (J. G. Moore, personal communication).

It has been suggested that the building of the volcanoes through the zone from a depth of a few thousand feet to sea level involved much steam explosion and granulation of the lavas in contact with water, producing large volumes of basaltic ash and hyaloclastite. Evidence from submarine photographs and dredging on the aforementioned rift zones does not

support this suggestion; but the evidence is scanty, and it has been argued that the fragmental material has been removed into deep water by currents. Certainly, however, in very deep water, explosion is prevented by the restraining pressure of the overlying ocean, though hyaloclastite formation might take place. The flows should be dense, because the restraining pressure prevents vesicle formation unless the gas content is very much greater than it is in magmas erupting above sea level. This theoretical conclusion is supported by the actual decrease in size and abundance of vesicles in samples of lava dredged from increasing depths of water.

All of the actual evidence suggests that the lower slopes of the volcanic mountains and the adjacent archipelagic aprons, as well as the sea floor at greater distances from the islands, consists of layers of dense tholeiitic basalt. A hole through the Moho in the Hawaiian region would give us our first real direct knowledge of the suboceanic "B layer."

Even less is known about the constitution of the mantle than about that of the suboceanic crust. Hawaiian alkalic basalts and nephelinites contain numerous inclusions of ultrabasic rocks, predominantly dunite, lherzolite, and wehrlite. Some workers have presumed these to be fragments derived from the mantle and carried up by the rising magma. However, at some localities they grade compositionally into gabbro, and even into anorthosite; and some show pronounced compositional banding closely resembling, if not identical with, that found in many big differentiated basaltic sheets such as the Stillwater intrusion in Montana. These are more probably derived from consolidated intrusive bodies at comparatively shallow depth beneath the volcano, well above the mantle boundary. Others may be derived from the mantle, though the evidence for this is slight and far from conclusive. Garnet pyroxenite ("eclogite") inclu-

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 86.

sions, found only at Salt Lake Crater on Oahu, show the garnet-omphacite association characteristic of high pressure, and appear probably to be of mantle origin; though it is conceivable that the conditions responsible for the development of the high-pressure mineral facies may have had some other origin.

Because of the very shallow position of the Mohorovicic discontinuity in the central Pacific, few persons still adhere to the belief that it may represent the basalt-eclogite phase transition (though a similar transition may take place from peridotite to olivine-garnet peridotite containing sodic pyroxene at a deeper level within the mantle). However, it has recently been suggested, on the basis of high P-T laboratory studies of basalt in the presence of volatiles, that the Moho beneath the deep oceans may be a phase transition from basalt to glaucophane-lawsonite rock (George Kennedy, address at Berkeley, California, October 7, 1964).

The net conclusion from all available evidence seems to me to be that the mantle beneath the central Pacific probably consists of peridotite approaching in composition the average stony phase of stony meteorites, or the theoretical "pyrolite" of Lovering, undergoing a phase change at depth to olivine-garnet pyroxenite.

In recent years a large amount of important petrologic theory and petrogenic speculation has been based on Hawaiian rocks. We are accumulating a large mass of information on the volcanic rocks above sea level. The evidence is strong that, whatever the processes that give rise to the diversity of rock types in Hawaii, the primary magma or magmas that give rise to them are derived from the mantle. Yet it should be obvious from the foregoing that very little is known directly of the composition of the mantle in the Hawaiian region. A hole through the Moho in this region would give not only incontestable knowledge of the nature of the mantle, but also specific knowledge of its local chemical and mineral composition that can be correlated with the composition of the extensively studied tholeiitic lavas found in Hawaii. Such correlative studies are essential if theories about the origin of magmas are to move out of the realm of speculation onto firmer ground.

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# Geochemical Studies of Hawaiian Rocks Related to the Study of the Upper Mantle<sup>1</sup>

JOHN J. NAUGHTON and I. LYNUS BARNES

CERTAIN ROCKS, notably ultramafics (peridotites) and eclogite, have properties which fulfill a good many of the criteria for the material of the upper mantle. Hawaiian lavas have served as model substances in these categories (specifically nodules from Hualalai, Hawaii, and eclogite from Salt Lake Crater, Oahu). In fact, Tilton and Reed (1963), on the basis of the factors contributing to radioactive heating, believe that Hawaiian eclogites are the best guides to the composition of the upper mantle. Other investigators (Engel and Engel, 1964) are of the opinion that tholeiitic basalt, which is the predominant lava type of the Hawaiian Island chain and is unique in its abundance at this site, is the chief or only magma generated in the earth's mantle under oceanic ridges and rises.

Geochemical investigations at the Hawaii Institute of Geophysics have contributed in several ways to the understanding of Hawaiian lavas as materials recently derived from the earth's mantle.

## AGE-DATING

Dating work has been directed mainly to investigations of the suitability of whole rocks for age-dating using the Waianae volcanics of Oahu, and to solving the problems of dating relatively young rock. Some preliminary results are listed in Table 1, giving an idea of the age range expected in Hawaiian lavas and the capabilities of the potassium-argon method for dating young rocks.

The results are in good agreement with the whole rock determinations of McDougall (1964). The discrepancy between whole rock and included mineral ages is under investigation and must be resolved before proceeding with further studies.

Using the convective cell theory (Wilson, 1963) and the distance from the present active source on Hawaii to the Waianae volcano, a crustal movement of about 10 cm/year has been calculated by McDougall (1964). If the age of included mica from the Waianae lower member is used (8 million years), a rate of 4 cm/year is found, which is in better agreement with the 3 cm/year calculated as the upper limit for convective currents in the upper mantle (McDougall, 1964). The alternate interpretation of these data of course is that the age relations reflect progressive development of volcanism along gradually developing fractures in the crustal mantle, rather than crustal migration from a single primary source of volcanism.

## ANALYSES FOR MAJOR AND MINOR ELEMENTS

A controversy has been under way for many years as to the possible source within the upper mantle of the two main types of oceanic lavas (tholeiitic and alkalic). One school maintains that they have two completely separate magma sources (Kuno, 1959), the other that both have been derived from a single parent magma by gravitational differentiation or by separation at a different stage of lava ascent (Engel and Engel, 1964). Seismic evidence in Hawaii indicates that the primary events which culminate in eruption at active volcanoes take place within the upper mantle at a depth of about 60 km, and that build-up and storage of lava occur in a magma chamber about 3 km immediately beneath the volcano (Eaton and Murata, 1960). Thus, the active sequences in Hawaii are relatively clear, and chemical and petrological studies on Hawaiian lavas have figured most prominently in the discussions of the theories of basalt derivation.

Chemical analyses of some hundreds of samples are available for Hawaiian lavas, with many

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 87.

TABLE 1  
AGES OF CERTAIN HAWAIIAN LAVAS

SAMPLES	AGES (in millions of years)
Older rocks (whole rock investigation)	
Lowest member dated, Waianae, Oahu	5.4
Low member, Waianae, Oahu (trachyte)*	3.46**
Upper member, Waianae, Oahu	2.8
Dike rock, Koolau, Oahu	2.2
Younger rocks	
Puuwaawaa trachyte, Hawaii	0.4
Laupahoehoe, Mauna Kea, Hawaii (whole rock)	0.6
Laupahoehoe, Mauna Kea, Hawaii, mica (mineral in Laupahoehoe whole rock)	2.8

\* Subject of many analyses on whole rock and minerals; indications are that minerals give older date.

\*\* Average of six determinations.

of the recent results coming from the Hawaii Institute of Geophysics. Using these analyses, the tholeiitic-alkalic dichotomy is readily recognized from the alkali content, and Macdonald and Katsura (1962) have developed the alkali-silica diagram as a quantitative means of differentiating the two types. In this diagram, when per cent alkali ( $K_2O$  plus  $Na_2O$ ) is plotted against per cent silica, the tholeiites occur as a well defined group in the lower part of the diagram and the alkalic lavas occur in the upper section. Standard A-F-M (Alkali-FeO-MgO) diagrams also show a distinctive grouping of rocks of the two types. The conclusions reached by Macdonald and Katsura (1962, 1964) from studies of the chemical composition of the analyzed samples are: (1) the primitive lavas that built the Hawaiian volcanoes are tholeiitic basalt; and (2), more tentatively, alkalic rocks can be derived from a tholeiitic parent.

A study of certain minor elements in tholeiitic and alkalic suites of Hawaiian lavas is being conducted (by G. A. Macdonald, N. J. Hubbard, and I. L. Barnes) with analyses being made by emission spectroscopy. To date 39

rocks from the Waianae range on Oahu have been analyzed for cobalt, nickel, vanadium, and zirconium. Results indicate that zirconium may be a distinctive trace element between suites, and, most interestingly, that when the nickel, vanadium, and zirconium contents are plotted in a tri-variant diagram, there is a grouping of results for rocks of the two types (tholeiitic and alkalic) similar to that noted in the A-F-M diagrams. Thus, it may develop that minor elements will prove to be distinctive markers for lava types.

#### VOLCANIC GASES

Volcanic gases supply a probe which enables a characterization of magma to be made at depth within the earth's crust, at least to the point of separation of gas from the parent lava. Once separated, such gases have been found to be a system in homogeneous equilibrium in the gaseous phase, and quite out of equilibrium with the associated rock system. Within error of measurement, analyzed samples of gas collected at high temperatures have been shown to conform to the composition expected thermodynamically for a homogeneous system. It is possible, then, to extrapolate the composition of gases collected during eruption to discover the oxidation condition of the underground magma, provided the temperature is known; or, conversely, for a given partial pressure of oxygen to find the temperature (Heald, Naughton, and Barnes, 1963). For a more complete analysis a computer may be used to calculate the compositional changes in a homogeneous volcanic gas system with expected changes in temperature, pressure, oxygen partial pressure, and the addition or subtraction of gaseous components which might be anticipated from surrounding rock (i.e., water vapor) (Heald and Naughton, 1962).

Using reasonable estimated values of temperature and pressure, it was concluded from data obtained from the best Kilauea samples that the primary magmatic gas would have the composition shown in Table 2.

Comparison of this calculated composition with the analyzed results from good collections made from liquid lava shows that an equilib-

TABLE 2  
COMPOSITION OF PRIMARY MAGMATIC GAS

COMPONENT	VOLUME % at 1500° K
H <sub>2</sub> O	62.5
H <sub>2</sub>	1.90
CO <sub>2</sub>	20.2
CO	1.66
H <sub>2</sub> S	0.38
SO <sub>2</sub>	13.2
S <sub>2</sub>	0.42

rium temperature of 1200°–1500°K is indicated for the actual gas. The value of the partial pressure of oxygen was found to be approximately  $10^{-8}$  atmospheres, in agreement with the value of  $10^{-6}$  to  $10^{-8}$  atmospheres estimated independently from the study of basaltic rocks (Fudali et al., 1961). Measurement of the oxygen partial pressure is significant in that this quantity has been shown to influence crucially the course of magmatic differentiation (Osborn, 1962), and may be the much-sought factor causing the derivation of different types of basalt from a tholeiitic parent magma. It will be noted that the magmatic environment found from these measurements is a reducing one.

#### MEASUREMENT OF RADIOELEMENTS IN LAVA

Hawaiian rocks have been used extensively in work on the very low uranium content of ultrabasic rocks and minerals, with the most recent researches on ultramafics and possible mantle materials being reported by Tilton and Reed (1963), and by Lovering and Morgan (1963). Also, a great deal of interest has centered on lead isotopic anomalies observed in researches on Pb–Pb, U–Pb, and Th–Pb dating methods (Russell and Farquhar, 1960). In explaining these anomalies, discussion has involved the uncertainties regarding the cogenicity of lead and uranium, and the processes which might lead to separation of these elements during derivation from the mantle (Marshall, 1958). Larson and Gottfried (1960) made some measurements on Hawaiian rock suites, and found uranium contents varying from 0.21 to 1.8 ppm. They find an increase in uranium content in late basaltic differentiates (alkali basalts). In general, as pointed out by Heier

and Rogers (1963), work on the uranium geochemistry of basaltic rocks has not been extensive.

At the Hawaii Institute of Geophysics work on the radioactivity of Hawaiian lavas is only in the preliminary stages of feasibility studies. Research with alpha-sensitive nuclear emulsions shows the uniform distribution of alpha activity in the groundmass of tholeiites, and the higher concentration of activity in alkali suite members. A study of disequilibrium in the uranium decay chain is underway with a measurement of lead –210 through its alpha-active polonium –210 daughter. Easily measurable activities are found, and alpha spectrometry will be applied in the study. The radon content of volcanic gas is being measured also.

Knowledge of the uranium, thorium, and potassium in Hawaiian lavas will enable estimates to be made of their contribution to the radioactive heat production, and an evaluation of a parent tholeiite magma as a reasonable direct derivative from the mantle which is in agreement with measurements of oceanic heat-flow.

#### ACKNOWLEDGMENT

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# Ultrasonic Velocities and Related Elastic Properties of Hawaiian Basaltic Rocks<sup>1</sup>

MURLI H. MANGHNANI and GEORGE P. WOOLLARD

LABORATORY MEASUREMENTS of the compressional-wave and shear-wave velocities of various rock types give a useful basis for understanding the geological significance of observed variations in seismic-wave velocities associated with the crust and upper mantle (Birch, 1961, 1964).

The rocks exposed at the surface in Hawaii provide excellent material for testing the velocity-density relationships and the anisotropic effects in rocks believed to form the crust and the upper mantle under the ocean floor. These rocks exhibit wide ranges of porosity, density, and mineralogical composition, and their physical properties represent a number of emplacement environments.

The Hawaii Institute of Geophysics program for measuring the elastic properties of the Hawaiian rocks is confined as yet to normal pressure and temperature conditions, but it is planned to expand the program to include studies under high pressure and temperature conditions to match those at depth down to the level of the lower crust and the upper mantle.

The following paragraphs present the results of measurements of density and ultrasonic velocities for some selected Hawaiian rocks which are significant in the interpretation of the crustal and upper mantle structure from seismic and gravity observations.

## METHOD OF MEASUREMENT

The pulse technique of measuring compressional-wave velocities described by Birch (1960) was the one employed in the present investigation. Shear-wave velocities were measured using the technique described by Jamieson and Hoskins (1963). Their method involves the use of P-wave transducers, the conversion of the P-wave pulse into an S-wave pulse through a

pyrex glass prism, transmittance of the S-wave through the sample, and reconversion of the S-wave into a P-wave through a similar prism. Barium titanate transducers were employed in making all measurements. In addition to cores, samples cut into cuboids of suitable dimensions ( $2 \times 2 \times 2$  inches) were used for measuring velocities in three mutually perpendicular directions.

## RESULTS AND DISCUSSION

The elastic properties of some of the Hawaiian basaltic rocks that were studied are given in Table 1. The rocks represented are tholeiitic and alkaline olivine basalts, trachyte, amphibolite, ankaramite, dunite, and eclogite. Basalts represent the largest group of rocks studied. The maximum compressional-wave velocity (7.0 km/sec) under surface conditions is found in an amphibolitic intrusive dike rock having a density of 3.0 gm/cc. This rock is found in the Koolau caldera. Another specimen (eclogite), also from the Koolau caldera, has a rather low density (2.81 gm/cc) and velocity (6.2 km/sec). In hand specimen the eclogite appears to be porous ( $>5\%$ ), and under the microscope it shows some alteration zones formed as a result of reaction with the magma during its eruption. Without this contamination the eclogite would have had a density and velocity equivalent to that found for the amphibolitic rock of the Koolau caldera. The significance of high density (3.0 gm/cc or higher) and high velocity (7.0 km/sec or higher) values is evident in that these materials truly represent, in terms of seismic velocities, the constituents of mantle-like material in this caldera. An ultrabasic rock with a surface density of 3.0 gm/cc and velocity of 7.0 km/sec, when placed in the upper mantle environment under the oceans (approximately a depth of 10–12 km), would have a velocity of 7.5–7.8 km/sec.

<sup>1</sup>Hawaii Institute of Geophysics Contribution No. 88.



TABLE 1  
ELASTIC PROPERTIES OF SOME HAWAIIAN BASALTS

SAMPLE	$V_p$ * km/sec	$V_s$ km/sec	$\epsilon$ (DENSITY) g/cc	$\kappa$ (BULK MODULUS) dynes/cm <sup>2</sup> $\times 10^{-11}$	$\mu$ (MODULUS OF RIGIDITY) dynes/cm <sup>2</sup> $\times 10^{-11}$	E (YOUNG'S MODULUS) dynes/cm <sup>2</sup> $\times 10^{-11}$	$\frac{\kappa}{\mu}$	$\sigma$ (POIS- SON'S RATIO)
Olivine basalt	4.95 4.63 4.82	2.56	2.0	3.15	1.31	3.45	2.40	0.317
Olivine basalt	4.65	2.50	2.30	3.05	1.47	3.80	2.07	0.292
Olivine basalt	5.65 4.38 5.47	3.10	2.36	4.03	2.27	5.23	1.78	0.264
Olivine basalt (ankaramite)	5.08	3.02	2.40	4.6	2.18	5.56	2.11	0.296
Olivine basalt	5.52	2.76	2.60	5.27	1.98	5.27	2.63	0.330
Eclomite	6.06 5.82 5.86	2.94	2.81	6.29	2.43	6.45	2.59	0.328
Amphibolite	6.90 6.75 6.76	3.53	2.95	8.5	3.67	9.63	2.32	0.312
Hawaiite	4.20	2.51	2.59	2.4	1.63	4.0	1.48	0.224
Trachyte	5.18	2.83	2.60	4.22	2.08	5.4	2.15	0.298

\* The three values of  $V_p$  are for transmission in three mutually perpendicular directions of propagation through the same specimen.

Figure 1 shows the velocity-density relation of the Hawaiian basalts and other volcanic rocks. These are primarily olivine basalts with varying amounts of olivine and other ferromagnesian silicates. The velocities of the olivine basalts vary from 4.5–6.5 km/sec with corresponding changes in densities from 2.2–2.8 gm/cc. As will be seen, the values are largely dependent on vesicular structure, the amount of interstitial glass present, and the amount of olivine present.

Figure 2 shows the variation in ultrasonic velocities in four olivine basalts of comparable density but having different percentages of olivine. The inclusions of dunites and olivine-rich rocks in some of the volcanic flows on the island of Hawaii, especially in the 1801 flow, are not

uncommon, and have been described by Ross et al. (1954). These rocks, composed principally of olivine, give velocities of 6.5–7.2 km/sec (density 2.8–3.1 gm/cc) under atmospheric conditions of temperature and pressure. Of all the Hawaiian rocks whose transmission velocities have been measured (including eclogite), the dunites and olivine-rich inclusions give the highest values. The measured seismic velocities of the upper mantle under the Hawaiian Archipelago (Furumoto and Woollard, p. 315 in this issue; Eaton, 1962) are of the order of 8.2–9.0 km/sec. Eaton's deduced velocity distribution under a typical volcano is based upon local earthquake data on Hawaii. The values reported by Furumoto et al. are based upon explosion seismic refraction measurements. In-

asmuch as most of the magmas connected with Hawaiian volcanic eruptions are believed to originate at the depths of earthquake foci at or about 60 km, the seismic velocities below the Moho are important from the point of view of the chemical composition of the upper mantle. Although it is not the purpose of this report to discuss the pros and cons of various models of the upper mantle, it can be said that the presence of olivine-rich nodules in some of the Hawaiian flows, the increasing transmission velocity of the olivine basalts (ankaramite) with increasing olivine content (see also Birch, 1961), and the seismic velocities of the layer below the Moho discontinuity (8.2–9.0 km/sec) all indicate that the upper mantle below the Hawaiian Archipelago is most probably composed of material resembling dunite. The planned high pressure and temperature measurements of velocities of the dunites and olivine-rich basalts at the Hawaii Institute of Geo-

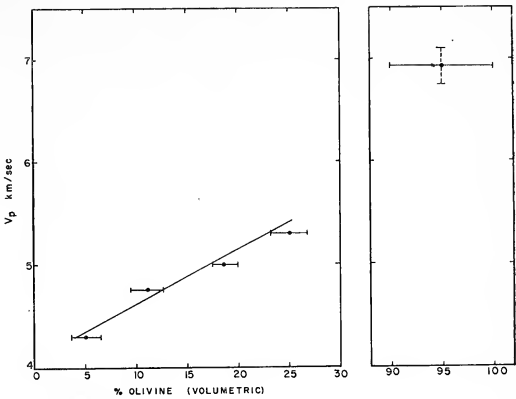


FIG. 2. Velocity versus olivine content in basalts.

physics should clarify some of the unsolved questions.

Amphibolitic rocks (Fig. 1, 1 and 2) and an eclogite (Fig. 1, 3) having higher densities than basalt show higher velocity values, as stated earlier. Although the curves of Figure 1 have been drawn on the basis of apparent porosity values as deduced from wet and dry density determinations, these are obviously not all true porosities and permeability is a parameter that is also incorporated. The effect of this factor will require further study. In gross form, though, the velocity-density relationships shown for volcanic rocks are essentially correct. As might be expected, the velocity in a rock is significantly lowered when the porosity increases. The dispersion in the three curves can be attributed to the differences in mineral composition, crystallinity of the material constituting the rock, the size and geometry of vesicles present, and the undetermined effect of permeability due to microfractures.

Horizontal variations in seismic velocities of the upper layers of the basaltic lavas on the Hawaiian Islands, as observed by the Hawaii Institute of Geophysics group (Furumoto and Woollard, p. 315 in this issue) and others, are real and thus signify variations not only in mineralogical composition and density but in vesicularity and permeability as well. Problems pertaining to the degree of vesicularity to be expected at depth can best be understood by studying the variation in seismic velocity in material of variable vesicularity and density. The ideal approach to the solution of this prob-

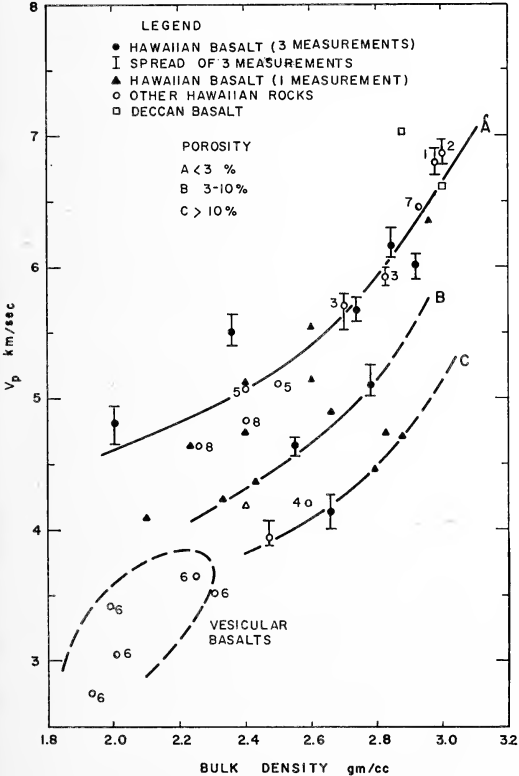


FIG. 1. Velocity versus density relationship in Hawaiian rocks. 1 and 2, amphibolitic rocks; 3, eclogite; 4, hawaiiite; 5, ankaramite; 6, vesicular basalt; 7, pyroxenite; 8, tholeiite.

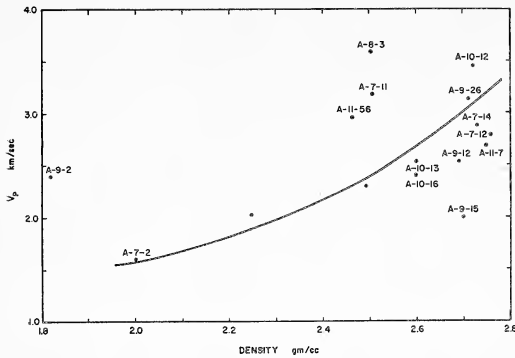


FIG. 3. Velocity versus density in cores from Alae Crater, Hawaii.

lem would be to drill through lava material and obtain the cores to examine vesicularity, density, chemical composition, and other physical properties. Figure 3 shows the physical measurements on some drill cores obtained from Alae Crater, island of Hawaii, by the U. S. Geological Survey Volcano Observatory scientists. Although there is a direct relationship between the velocity and density of these cores there is significant variation in the velocities of cores (Fig. 3, A-9-15, A-10-16, A-10-13, A-9-12, A-11-7, A-7-12, etc.) with little or no change in density (2.6–2.7 gm/cc). The chemical composition of these cores is about the same (Dallas Peck, personal communication), but there is a large variation in the glass content in the rock material. Because the modulus of rigidity of glass is much lower than the average value of equivalent crystalline rock material, the velocity of propagation of elastic waves will be lowered as the percentage of glass increases. The relationship between velocity and glass content for these cores is shown in Figure 4. The low velocities of the Pacific Ocean upper crustal layer (3.8–4.2 km/sec) reported by Raitt (1956), and by Shor and Pollard (1964), and verified by the unpublished studies by Western Geophysical Company, suggest that the glass content may be influencing the seismic velocity to a large extent. Certainly, the work by J. Moore of the U. S. Geological Survey (personal communication) indicates essentially zero porosity for basalts extruded on the ocean floor. Quick chilling could produce interstitial glass, however.

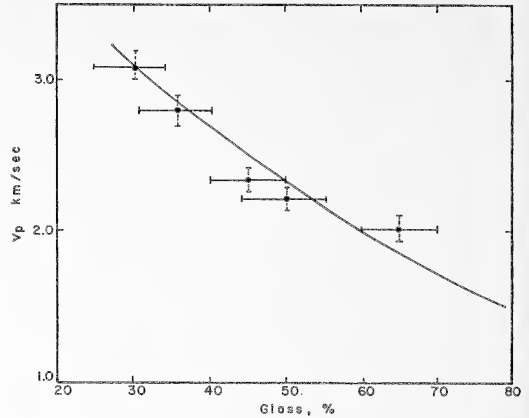


FIG. 4. Velocity versus glass content in cores from Alae Crater, Hawaii.

ANISOTROPY

There is a significant degree of anisotropy in the transmission of compressional waves in Hawaiian rocks. This is shown in Table 1 and Figure 1, where velocities obtained in three perpendicular directions through the same sample are recorded. In some rock types there is as much as 8–10% difference between the maximum and minimum velocities observed. Although anisotropism in vesicular lavas is related to dimensional orientation of the vesicles, in whole rock material it is related principally to mineral orientation. Both olivine and plagioclase feldspars are of special interest in the interpretation of seismic refraction data. This portion of the study now underway at the Institute of Geophysics is still in its initial stage.

SUMMARY

1. Density, rock structure, porosity, permeability, and glass content control the seismic velocities of the vesicular basaltic lavas.
2. Density, glass content, and mineralogical composition of the non-vesicular flows and intrusives control their seismic velocities and related elastic properties.
3. The alkalic basalts (e.g., trachytic type) have a low velocity of transmission as compared with the tholeiitic olivine basalts.
4. The average value of Poisson's ratio for Hawaiian basalts is 0.29.

5. Dunites and olivine-rich inclusions in the Hawaiian basalts have the highest transmission velocities observed in this study. This material is most probably derived from the upper mantle.

6. The Hawaiian rocks exhibit significant degrees of anisotropy due to the differences in the mineral composition and orientation, and the geometry and orientation of the vesicles.

#### ACKNOWLEDGMENTS

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# A Seismic Refraction Study of the Koolau Volcanic Plug<sup>1</sup>

WM. MANSFIELD ADAMS and AUGUSTINE S. FURUMOTO

**ABSTRACT:** The seismic data from the GASHOUSE line support the gravity and magnetic data as indicating a plutonic body occurring beneath the center of the Koolau caldera in the vicinity of Kailua, Oahu. This plug has a velocity greater than 7 km/sec and adjoins material with a velocity of about 4.6 km/sec at the top and to the southeast. The width of the plug is estimated to be about 6 km down to 3–4 km. Reflections from a horizon greater than 3 km deep may indicate an underlying magma chamber. The top of the plug is about 1600 m deep.

Drilling of this plug would have considerable scientific value both geologically and geophysically. An appropriate drilling site would be at the southwest corner of Kaelepulu Pond, which lies close to the center of the plug as now defined geophysically. Seismic reflection work directly above the dome is also recommended to test the present estimate of the depth based on refraction results.

GRAVITY MEASUREMENTS on the windward side of Oahu define a local anomalous high of about +110 mgal. This was first reported by Woollard (1951), and subsequently has been surveyed in more detail by the Institute of Geophysics. Woollard interpreted this anomaly as being caused by high density (3.2–3.3 g/cc) pipe material extending to within 1–2 km of the surface. A more recent analysis (Strange, Woollard, and Rose, p. 381 in this issue) arrives at much the same conclusion. Although the initial intention of the seismic work reported here was to “fan shoot” the plug, as well as to determine its velocity and depth, the over-all difficulty of the experiment and higher-than-anticipated costs dictated that part of the operation be curtailed. It was decided that the depth and velocity of the plug—as possible mantle material—was of greater interest than the extent. Therefore, all work has consisted of in-line refraction shooting in order to obtain estimates of the seismic velocity in the plug and the depth to the top of the plug.

## PREDICTION TECHNIQUE EMPLOYED

Previous seismic work on plugs has been concerned mostly with exploration for oil around salt domes. The objective in such work is to

define the flanks of the dome so that exploratory drilling can be conducted. There is very little interest in the velocity or shape of the top surface of the dome, and a satisfactory estimate of the depth of the dome can usually be obtained from reflections or from potential methods since the density of salt is quite uniform from dome to dome. Investigations of buried volcanic plugs have been few and mostly unsuccessful. Thus, the present investigation is relatively unique in that it appears to have been a success. This can be attributed in large part to planning of the field work.

A theoretical model was first constructed based on the gravity estimates of the depth and size of the plug and seismic velocities determined from short exploratory refraction spreads. The model used is shown in Figure 1. The velocities at depth were taken from preliminary estimates on the ABLE line running to the northwest along the northern shore of Oahu (Furumoto, Thompson, and Woollard, p. 306 in this issue). The features in the resulting theoretical travel-time curves are the usual crossovers, but with the 6.2 km/sec leg being shifted downward at greater distance, similar to that which occurs on the down-thrown side of a normal fault (see, for example, Nettleton, 1940:272). In addition, there are later arrivals in the region of the start of the downward diffraction distance

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 89.

and usually at shorter distances, which correspond to head waves that are refracted upward from the top of the plug. It is these head waves which permit an estimate of the velocity in the plug.

Note that this program was initiated with the expectation that the data desired would occur as second arrivals. It should also be noted, however, that if the plug extends upward to a sufficiently shallow depth, then the refraction segment will move downward across the 6.2 km/sec leg and actually be composed of the first arrivals. In this case, the end of the refraction segment would still taper off into the diffraction zone. Another point of interest in connection with this model is that if the plug does

not completely penetrate the 6.2 km/sec layer, double arrivals at distances greater than the diffraction distance are to be expected. If the plug does completely penetrate this layer, then the 6.2 km/sec leg would not be extended.

FIELD PROGRAM

A location map of the area of interest is shown in Figure 2. The other seismic lines established by the Hawaii Institute of Geophysics—ABLE, BRAVO, and DELTA—are also shown. The area of interest is denoted by the block oriented NW–SE. This is shown in detail in Figure 3.

The gravity high defining the Koolau caldera lies on the present coastline and adjoins Kaneohe Bay. Because the caldera is now a residential area, Kaneohe Bay provided the only feasible area for shooting charges large enough to obtain data over the ranges required. The initial field effort was confined to the caldera, but it soon became apparent that operations restricted to this area would not yield satisfactory data because of the slope-effect of the buried caldera walls, which on some spreads resulted in infinite apparent velocity values. The shot line finally established based on the model analysis extends across the center of the gravity high with relatively slight deviations of stations from a straight line, except in the vicinity of Kawainui Swamp where transportation was restricted. An effort to use U. S. Marine personnel carriers to work straight across the swamp ended in failure when the vehicles became hopelessly bogged down.

All the shots that were conducted for recording along this line are listed in Table 1. Each shot was recorded with 250-ft spreads at two positions. Each shot consisted of 50 lb of Nitramon detonated on bottom at a depth of 50 ft at the location of Buoy 27 in Kaneohe Bay. It was hoped that shooting on bottom would give maximum seismic energy coupling and minimize the bubble pulses (Worzel and Ewing, 1948:18). Larger charges could not be shot due to cultural restrictions.

The usual field difficulties due to imperfections of men and machines were encountered. Sample records are shown in Figure 4. The paper speeds used were 2 inches/sec or 8

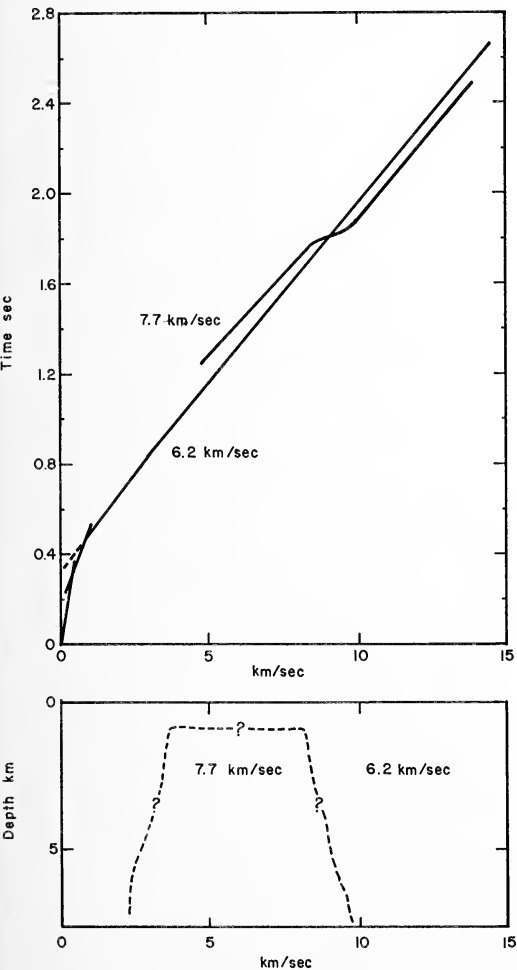


FIG. 1. Structural model used for planning seismic field effort.

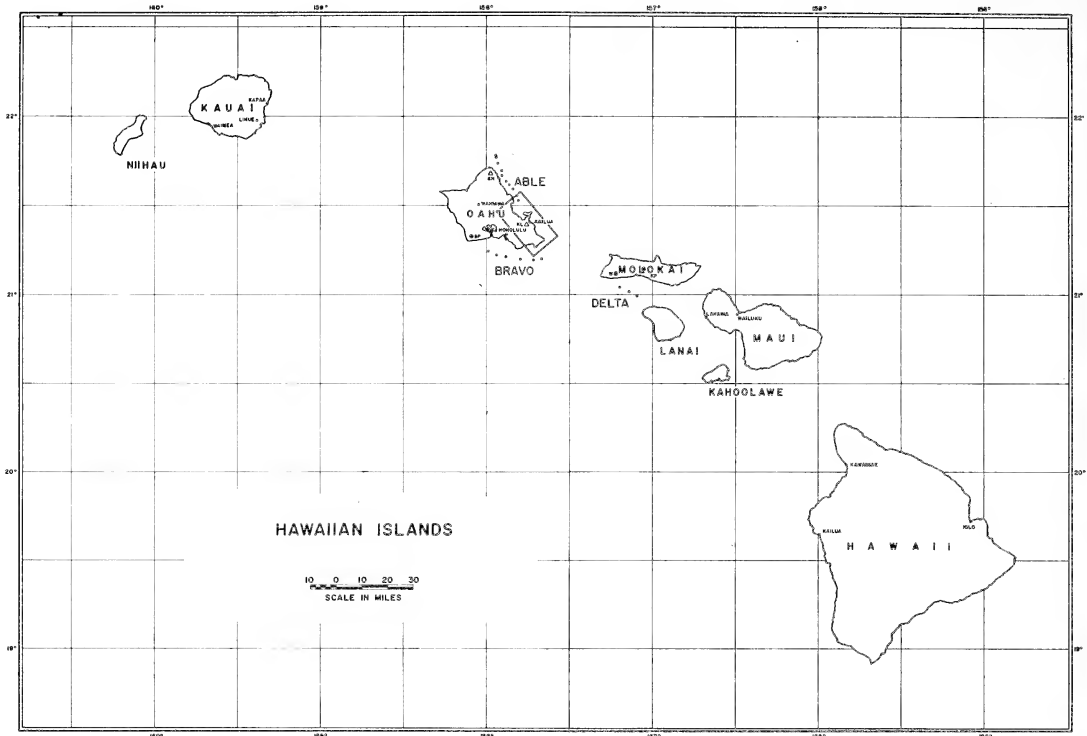


FIG. 2. Location map of the seismic field program.

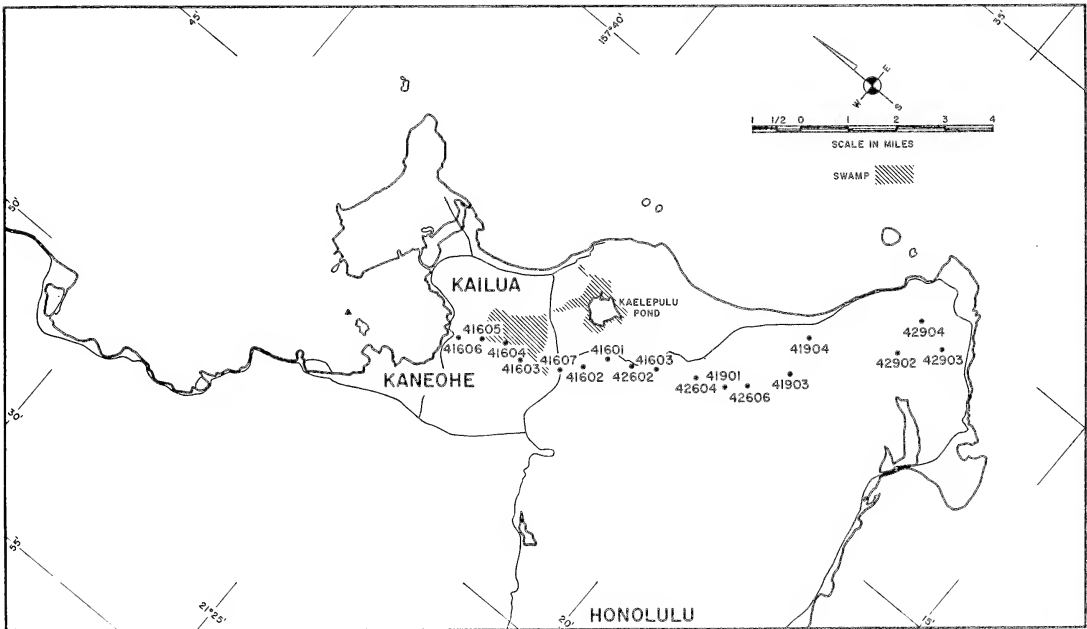


FIG. 3. Location map of the field stations in the vicinity of Koolau caldera.



inches/sec. Some of these records will be referred to later, under the section on interpretation, as they are critical to the analysis.

Important travel-time picks taken from the seismograms are listed in Table 2. Although the values are given to a millisecond, the data are not necessarily reliable to better than 10 milliseconds. Because of the short spread-length (250 ft) necessary, apparent velocities are not given as they are not regarded as having any real significance.

INTERPRETATION OF DATA

The writers' interpretation of the data is presented in Figure 5 as a standard travel-time graph. The sample record locations are noted, and the reader should refer to them as needed while reading the remainder of this section on interpretation. The present interpretation is not the first derived, nor the one presented by Furumoto at the Eastern Section of the Seismological Society of America (Furumoto, 1964).

The change in interpretation resulted from subsequent additional shooting.

The most prominent feature on the records and on the travel-time plot of the data is the strong, frequent occurrence of a second arrival about 0.450 sec after the initial motion. This has been interpreted as being a bubble pulse. The theoretical time-delay value that should be obtained for a shot in a 50-ft depth of water, neglecting the bottom effects, can be obtained from the equation

$$T = 4.19 \frac{W^{1/3}}{(H + 33)^{5/6}}$$

where H is the depth in feet of the shot point, and W is the weight of explosive in pounds. From this calculation, we obtain 0.368 sec, which is considered to be in satisfactory agreement with the observed interval of 0.45 sec since bottom effects have been ignored. From the sample record corresponding to a distance of 3.79 km (Fig. 4), the similarity of the bubble pulse to the initial motion in both ampli-

TABLE 1  
TIME AND LOCATION OF SHOTS FOR THE SEISMIC REFRACTION STUDY\*

SHOT NO. **	DATE	TIME	WHITE TRUCK		GREEN TRUCK	
			Distance (km)	Elevation (ft, ± 5 ft)	Distance (km)	Elevation (ft, ± 5 ft)
4T601	10/1/64	0929	7.99	190	not recorded	
4T602	"	0932	not recorded		8.78	280
4T603	"	1021	5.94	140	9.62	260
4T604	"	1103	5.35	0	10.43	40
4T605	"	1145	4.55	40	11.70	140
4T606	"	1230	3.79	20	not recorded	
4T607	"	1330	7.27	100	13.51	95
4T901	11/15/64	1330	12.70	100	not recorded	
4T902	"	1400	not recorded		18.10	40
4T903	"	1450	14.80	200	19.50	90
4T904	"	1540	15.20	400	18.90	70

\* All charges were 50 lb at 50 ft deep in 50-ft depth of water (on bottom).  
\*\* T = 1 for white truck, 2 for green truck.

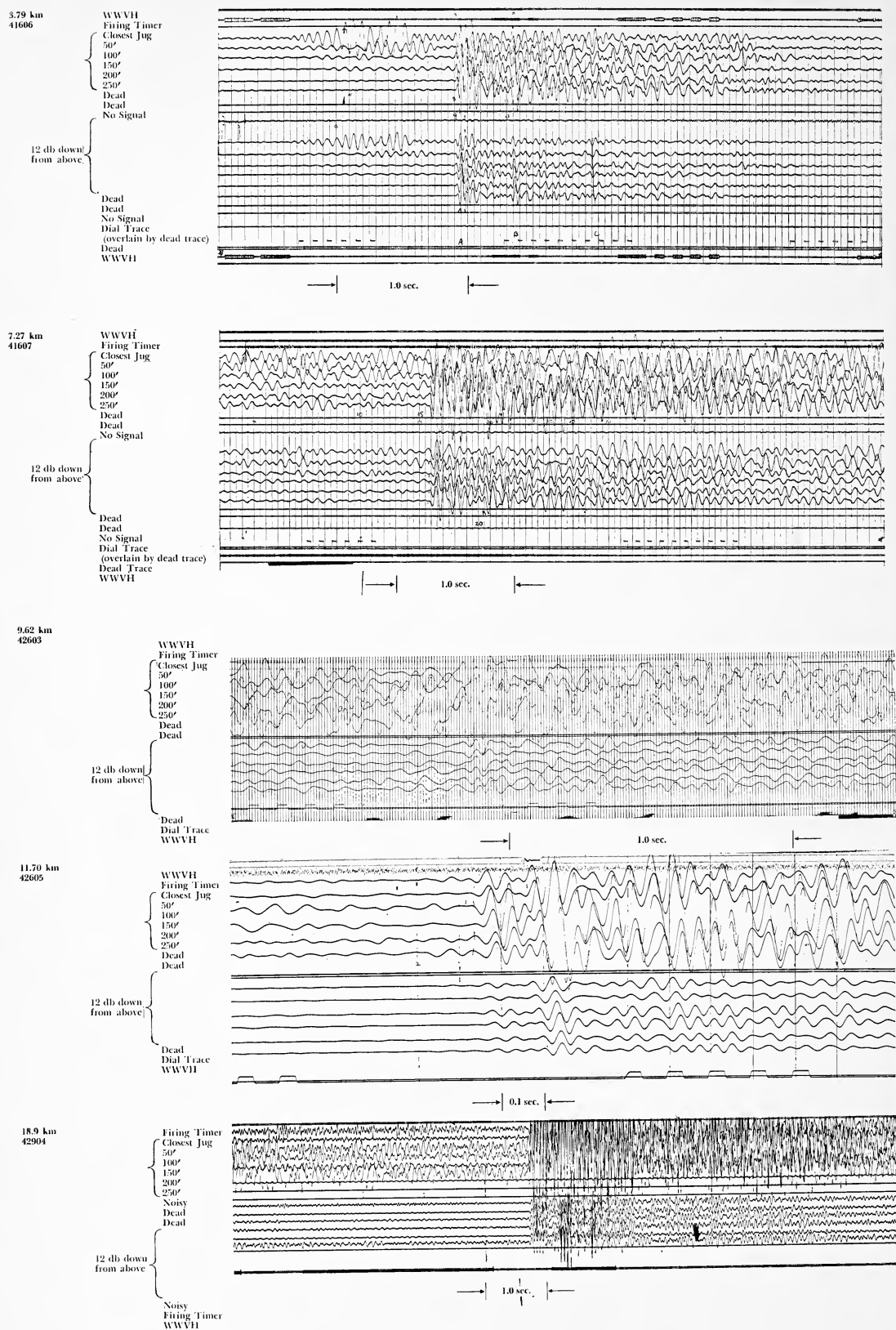


FIG. 4. Sample records taken in the refraction field effort.

rude and character can be seen. This occurrence of strong bubble pulse was especially annoying in this study in which secondary arrivals were expected to play a prominent part in the results.

From the travel-time plot, it is seen that the first arrivals align well out to 7.27 km. Beyond this point this line can be extended on the basis of secondary arrivals at distances of 8.8 km, 12.7 km, 18.1 km, etc.

The portion of the plot showing a downward shift in the arrival of first motion, initially attributed entirely to diffraction effects, is composed of notably strong arrivals and the bubble pulses duplicate the first motion in this sector. The segment of first motion from 11.7 km outward is definitely early and is parallel to the 4.74 km/sec segment obtained at distances less than 7.27 km. Considering the complexity of the

geology in a volcanic terrain, this extreme parallelism was unexpected. (Note, however, that the arrivals at 15.2 km are about 0.085 sec late for both the initial signal and bubble pulse, and that the arrival at the 19.5 km station is 0.123 sec late. Note also that the first arrival at 19.5 km, denoted with a question mark, was definitely a repick and was similar in character to noise in the leading part of the seismogram.)

The computer program for obtaining the best fitting line by least squares has been run on the first arrivals, the bubble pulses, and the early first arrivals. The values obtained are given in Table 3.

Assuming that the top of the plug is approximately parallel to the surface of the ground, the dependency of the first occurrence of refrac-

TABLE 2  
ARRIVAL TIMES FROM THE REFRACTION SEISMOGRAMS

DISTANCE (km)	RECORD NO.	1ST ARRIVAL (sec)	2ND ARRIVAL (sec)	3RD ARRIVAL (sec)	4TH ARRIVAL (sec)
3.79	41606	0.840	1.260	1.845	....
4.55	41605	0.960	1.398	1.870	....
5.35	41604	1.155	1.290	1.610	1.940
5.97	41603	1.295	1.505	1.770	2.090
7.27	41607	1.560	1.755	2.060	2.770
7.99	41601	1.640	1.800	2.140	2.380
8.78	42602	1.790	1.910	2.240	2.500
9.62	42603	1.848	1.948	2.288	....
10.43	42604	1.988	2.408	2.758	2.848
11.70	42605	2.115	2.270	2.470	2.970
12.70	41901	2.310	2.730	3.010	3.720
13.50	42607	2.495	2.778	2.875	3.375
14.80	41903	2.790	2.890	3.140	3.270
15.20	41904	2.950	3.140	3.350	3.540
18.10	42902	3.520	3.642	4.050	4.350
18.90	42904	3.680	4.090	4.180	4.580
19.50	42903	3.920	4.290	4.570	4.940

tions upon the depth to the plug and the seismic velocities in the plug and the overlying material can be determined (Fig. 6).

In this analysis we note that for the critical angle ( $i_c$ )

$$\sin i_c = \frac{V_o}{V_p}$$
$$\text{and} \quad \tan i_c = \frac{h}{H}$$

where  $H$  is the thickness of the layer and  $h$  the half distance from the point of origin to emergence.

Or if  $h$  is observed

$$h = H \tan \left[ \sin^{-1} \left( \frac{V_o}{V_p} \right) \right]$$

then

$$H = h / \tan \left[ \sin^{-1} \left( \frac{V_o}{V_p} \right) \right]$$

If the plug is of only limited lateral extent, then the diffractions off the trailing edge of the plug will start with the end of the segment of refracted arrivals and cross over the first arrivals to lead into the early portion of the early arrival segment. If, however, the plug is of sufficient

lateral extent, then the refraction segment representing the energy traveling through the plug will overtake the first arrivals and may even be composed of the first arrivals. The first case is illustrated in Figure 1, used to predict the expected results; the latter is seen in Figure 5, the interpretation made here. The strong energy in the first motion in the "diffraction" range supports this interpretation.

Based on the slope of the first arrivals at the downward flexure of the travel-time curve, a lower bound of 6.98 km/sec (say 7 km/sec) is obtained for the velocity in the plug. Inspection of the data in Figure 5 on which this is based indicates the relatively poor quality of the estimate.

An estimate of the depth of the dome at the point where the critically refracted ray enters can be obtained by the construction of the aplanatic line in the vertical plane containing both the shotpoint and the detector at the crossover station, 7.27 km. This has been done and the maximum depth is indicated as being 1630 m. This point corresponds to the point of the aplanatic curve which would be intersected by a ray leaving the origin at  $42^\circ$ , hence it is taken to be the depth. The reliability of this depth, then, depends on the validity of the assumption that the top of the plug is hori-

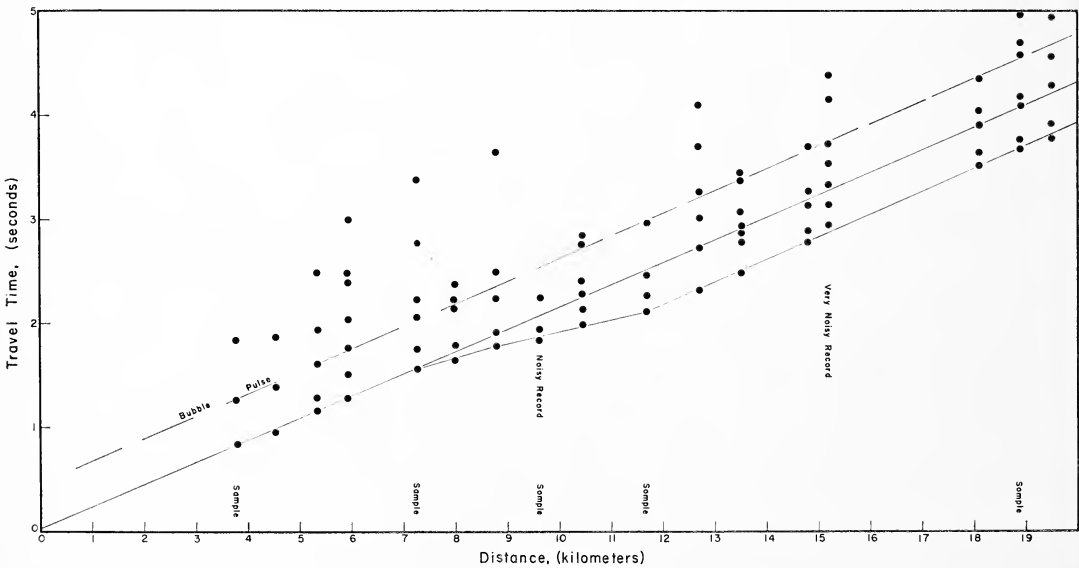


FIG. 5. Interpretation of the travel-time data.

TABLE 3

VALUES OBTAINED FROM COMPUTER PROGRAM RUN ON FIRST ARRIVALS, BUBBLE PULSES, AND EARLY FIRST ARRIVALS

COMPUTER CODE PARAMETER	UNITS	FIRST ARRIVALS	BUBBLE PULSES	EARLY FIRST ARRIVALS
K		1	3	4
N		5	9	6
X BAR	km	5.38	9.49	14.95
T BAR	sec	1.16	2.49	2.83
T RECIP	km	42.25	43.55	42.37
T NULL	sec	0.025	0.453	-0.363
SLOPE	sec/km	0.211	0.216	0.214
APP VEL	km/sec	4.74	4.64	4.68
VAR SLP	(km/sec) <sup>2</sup>	0.	0.	0.
DEV SLP	km/sec	0.	0.	0.
XDELTA	km	0.	582.25	-448.66

zontal at the point where the critically refracted ray enters. To be conservative in the following developments, we will use the value of 2 km. Actual drilling, however, should intersect the high velocity rock at less than 1630 m.

An estimate of the structure to which the observed travel times correspond is given in Figure 7. This should be compared with the

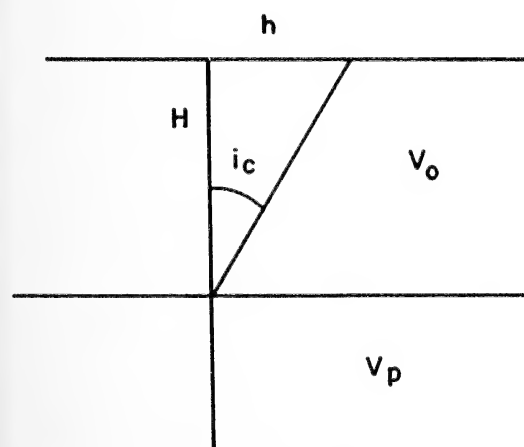


FIG. 6. Relation of refraction arrival section to position of the plug.

preliminary interpretation of line ABLE (Furumoto, Thompson, and Woollard, p. 306 in this issue), northwest from Kailua School, as the velocities obtained in that study have been used to guide this work. Note that the high velocity layer of about 6 km/sec was not observed to the southeast of the pipe in this present study. Because of this, one might be inclined to interpret the data as normal faulting, with the downthrown block on the southeast side. This is impossible because of the high energy arrivals observed in the 3- to 6-km range and arriving after the bubble pulse. These are interpreted as reflections off a possible former magma chamber at a depth of 3-4 km.

An alternative interpretation might attempt to fit the strong reflections arriving at short range with the bubble pulses in the intermediate range and make claim for a high-speed layer. Fortunately, the present survey was continued out to a distance from the shot point sufficient to preclude that possibility. Such a high-speed layer is not possible.

Since secondary arrivals still occur after the diffraction range, corresponding to direct arrivals through the 4.74 km/sec zone, the plug

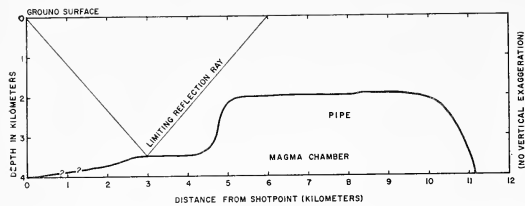


FIG. 7. Structure deduced from the observed refraction data.

does not penetrate the 4.74 zone. As can be seen from the sample record at 7.25 km, the first arrival is especially strong and probably corresponds to the intersection of the direct and the refracted waves.

Using the analysis corresponding to Figure 6 and assuming a depth of 2 km, we obtain an offset for the refracted data of about 1½ km. An estimate of the width of the plug may be obtained from the lead of the early arrival segment occurring after 11.7 km. This segment leads the extension of the previous first arrival curve by 0.410 sec. The meaning of this time lead can be seen from Figure 8.

Two rays are considered traveling from the source, S, to the observer, O, with one passing just above the plug and the other passing through the top of the plug. If we write the time of transit for the upper path as  $T_u$  and the time in the lower path as  $T_l$ , then

$$T_u = \frac{\overline{SO}}{V_o}$$
$$T_l = \frac{\overline{SO} - L}{V_o} + \frac{L}{V_p}$$

where  $\overline{SO}$  is the over-all path distance,  $L$  the width of the plug,  $V_p$  is the velocity in the plug, and  $V_o$  is the velocity in the matrix rock. The difference in arrival time will, therefore, be

$$T_u - T_l = L \left[ \frac{1}{V_o} - \frac{1}{V_p} \right]$$
$$T_u - T_l = L \left[ \frac{V_p - V_o}{V_o V_p} \right]$$

or

$$L = \left[ \frac{V_o V_p}{V_p - V_o} \right] (T_u - T_l)$$

This approximation assumes that the depth of the plug is negligible. If the top of the plug is moved downward, then the width of the plug must be increased.

Using this equation, the observed velocities, and the observed travel-time lead, we obtain a width for the plug of 5.4 km, which agrees closely with the surface geological indications of the size of the caldera and the gravity solution (Strange, Woollard, and Rose, p. 381 in this issue).

Some control on the horizontal position of the plug exists in the present data. The previously mentioned reflections occurring at about 2 sec after the shot time in the distance range 3.8–6 km correspond to reflections from a depth of about 3 km outside the boundary of the plug, as shown on Figure 7. This, incidentally, is of the same order as the depth extrapolated for the magma chamber under Kilauea by Eaton (1962). Therefore, we tentatively identify these as being from an existing or former magma chamber.

Assuming a geometrical ray path, one can obtain an inner bound from the onset of the effect of the plug. The plug effect would then persist along the line for about 5 or 6 km. There is some additional constraint on the outer limit from the critical angle at which the refraction from the plug occurs. The critical angle to the plug is about 41° for the velocities used here, so the refractions from the high velocity layer extend beyond the outer edge of the dome to a distance roughly equal to the dome's depth. This corresponds in the present case to a point about 11.7 km from the shot point. For a model depth of 2 km, the top of the plug begins to curve downward at about 10 km from the shot point along the recording line.

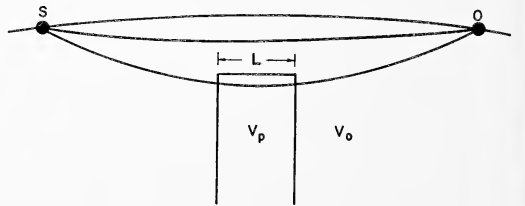


FIG. 8. Relation of transit times for paths inside and outside the plug.

The velocities observed here should be compared with those obtained by Manghnani and Woollard (p. 291 in this issue) on ultrasonic measurements of Hawaiian rocks, and with seismic velocities obtained by Raitt (1956), Shor and Pollard (1964), and the Western Geophysical Company (unpublished).

Current refraction work by the U. S. Geological Survey on the island of Hawaii substantiates the results of Eaton (1962) with respect to velocity and depth (D. Hill, personal communication). The Koolau caldera is somewhat unusual compared with those on the island of Hawaii because the gravity and magnetic anomalies are concentric to the geologic expression of the caldera. On the island of Hawaii the gradients are lower, indicating a greater depth to the plug, and the anomalies are usually shifted southward, usually in a greater amount for the older calderas. Only at Kilauea do the anomalies appear to be nearly concentric with the surface caldera.

#### ACKNOWLEDGMENTS

This work was possible only because of the persevering efforts of the following workers in the field: William Ichinose, Kenneth Hiraki, Lafayette Maynard, Wayne Lu, David Schla-

bach, Loren Kroenke, Monroe Woollard, and Noel Thompson. Interpretation was facilitated by discussions with George P. Woollard. Financial support was provided, in part, by NSF Grants GP-2257 and GP-3473.

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# The Structure of Koolau Volcano from Seismic Refraction Studies<sup>1</sup>

AUGUSTINE S. FURUMOTO, NOEL J. THOMPSON, and GEORGE P. WOOLLARD

THE ISLAND OF OAHU in the Hawaiian Archipelago was formed by the coalescing of two volcanoes, Waianae Volcano on the west and Koolau Volcano on the east. Both volcanoes have been dormant for tens of thousands of years. Erosion and weathering have cut deeply into them so that present topography does not clearly indicate the former shapes and sizes of the volcanoes.

A gravity survey by Woollard (1951) showed unusually high Bouguer anomalies over the caldera sections of both volcanoes. These high anomalies have whetted the interests of geophysicists, and recently projects were planned to make a detailed survey of the Koolau Volcano, using whatever geophysical and geological methods were available. In the fall of 1963 and the winter of 1964 intensive gravity surveys (Strange, Machesky, and Woollard, p. 350 in this issue) were carried out over the volcano. An aerial magnetic survey (Malahoff and Woollard, 1965) was carried out during the spring and summer of 1964. After information and data from the gravity and magnetic surveys became available, seismic refraction profiles were planned and carried out during the fall of 1964.

The prominent features of the Koolau Volcano are the caldera area, the northwest rift zone, and the southeast rift zone. From surface geology the existence of the northwest rift zone and the caldera was known (Stearns and Vaksvik, 1935; Stearns, 1946). Gravity surveys (Strange, Woollard, and Rose, p. 381 in this issue) later confirmed the findings by surface geology for the caldera area, but showed that the northwest rift zone was farther to the east than had been indicated by geology and topography. The southeast rift zone became known only after the gravity surveys.

## INSTRUMENTATION

Because mobility was necessary for the planned seismic refraction program, the recording units were housed in trucks. The trucks contained recording cameras, amplifier banks, portable box-type darkrooms, communications gear, geophones, and other accessories to set up a recording station.

The geophones were Hall-Sears geophones, with a natural frequency of 4.5 cps. Most of them were vertical components, but a few horizontal components were used. A typical spread consisted of six geophones in line, with 50-ft spacings.

The amplifiers were model type T-1, manufactured by Fortune Electronics. These completely transistorized amplifiers with low power consumption were found to be very satisfactory in field operations.

The recording cameras were manufactured by Southwest Industrial Electronics, Ltd. These cameras contained sufficient channels to record the signals from the six geophones at two different dynamic levels.

Communication between the recording trucks and the shooting party was done usually through Citizen's Band transceivers. The all-important shot instant was also transmitted by Citizen's Band transceivers by an audio tone beginning at the shot instant.

The firing of the explosives was done by a device, familiarly called the "tricky ticker," which in essence is a break-circuit chronometer operating a fixed sequence of audio tones and switches for firing. Details of the firing equipment may be found in Steinhart and Meyer (1961:158-163).

## FIELD WORK AND DATA PROCESSING

The seismic refraction traverses carried out for the project are shown in Figures 1, 2, and 3. Figure 1 shows the traverses designated by code

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 90.

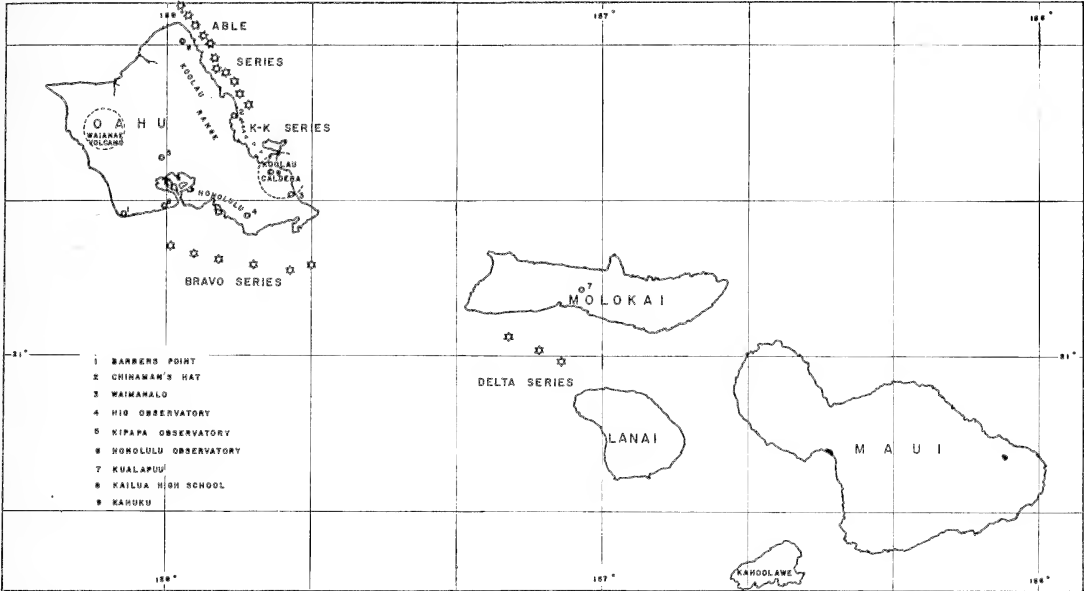


FIG. 1. Map of the Hawaiian Islands with locations of seismic refraction traverses and recording stations.

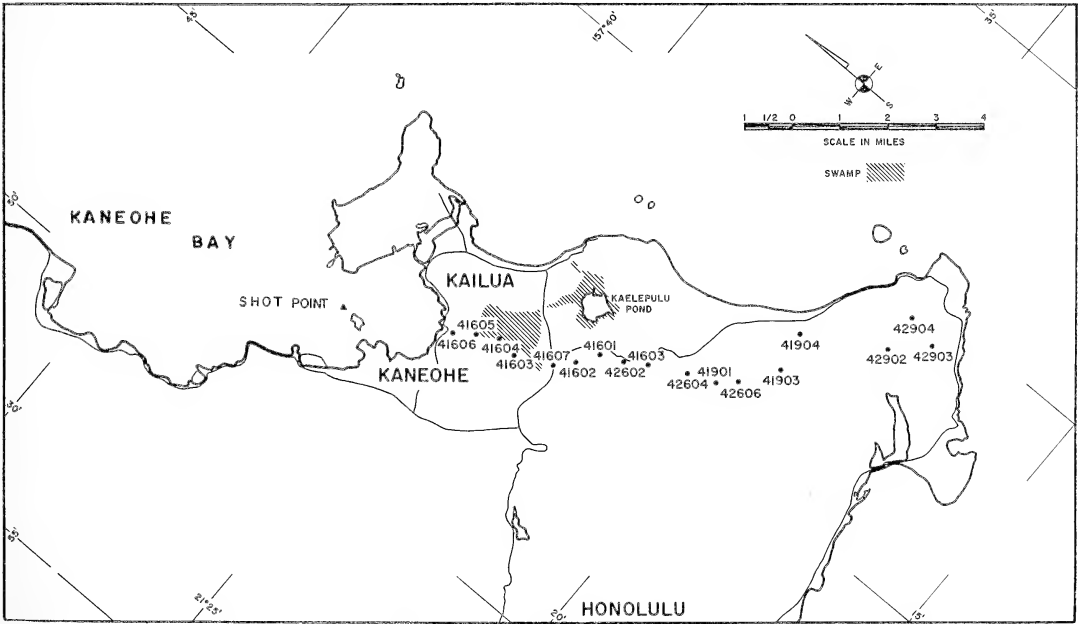


FIG. 2. Map of Koolau Caldera with shot point and recording stations for GASHOUSE series.

names ABLE, BRAVO, DELTA, and K-K; Figure 2, traverse GASHOUSE; and Figure 3, the shorter traverses in the caldera area to probe for shallow structures.

In the longer traverses of ABLE, BRAVO, DELTA, and K-K the explosives were set off under water at sea. The technique of fixed recording stations with moving shot points was used. For the K-K series the shooting crew operated from outboard motorboats because the largest charge-size amounted to 40 lb of TNT. For the ABLE, BRAVO, and DELTA series, the 85-ft R/V "Neptune I" of the University of Hawaii was used as a shooting platform because the charge-size used was large—either 200 lb or 500 lb of nitromon. For the K-K series the charges were detonated at the bottom of the bay, which on the average was 40 ft deep. For the ABLE, BRAVO, and DELTA series all shots were fired 75 ft below the water surface.

In the GASHOUSE series (Fig. 2) a fixed shot in Kaneohe Bay on the north side of Oahu was used while the recording trucks moved in a southeast direction away from the shot point.

In a number of short traverses to probe for the shallow structures of the caldera area, charges ranging from ½-lb blocks of TNT to 35 lb of nitromon were detonated in a drainage canal cutting across Kawainui Swamp which is located in the caldera area. For these short traverses the technique of fixed recording units and moving shot points was used. The shooting crew operated from shallow-draft rowboats.

Some rapid analyses of data were done in the field to judge whether data being gathered were adequate. The bulk of the data, however, was processed at the Hawaii Institute of Geophysics after the field work had been completed.

In data processing the seismograms were first examined and arrival times were picked by eye. After rough travel-time graphs were plotted

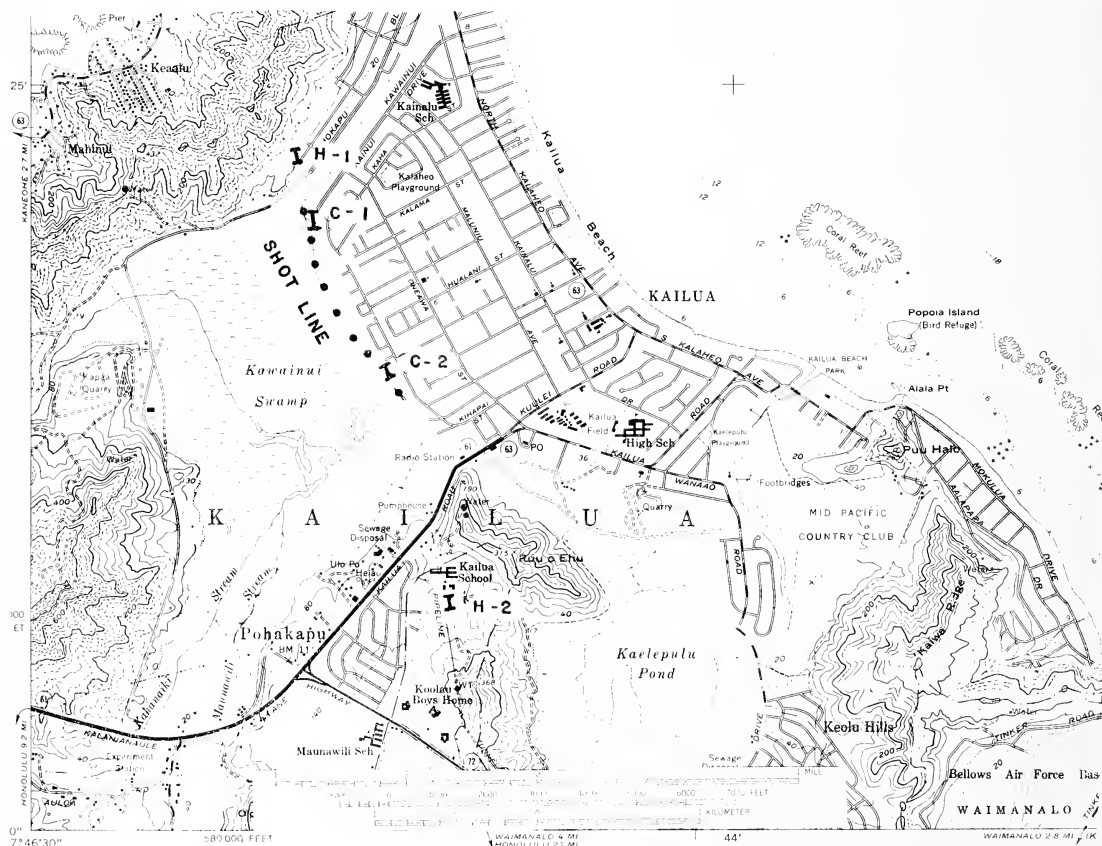


FIG. 3. Location map of refraction traverse and recording stations near Kawainui Swamp.

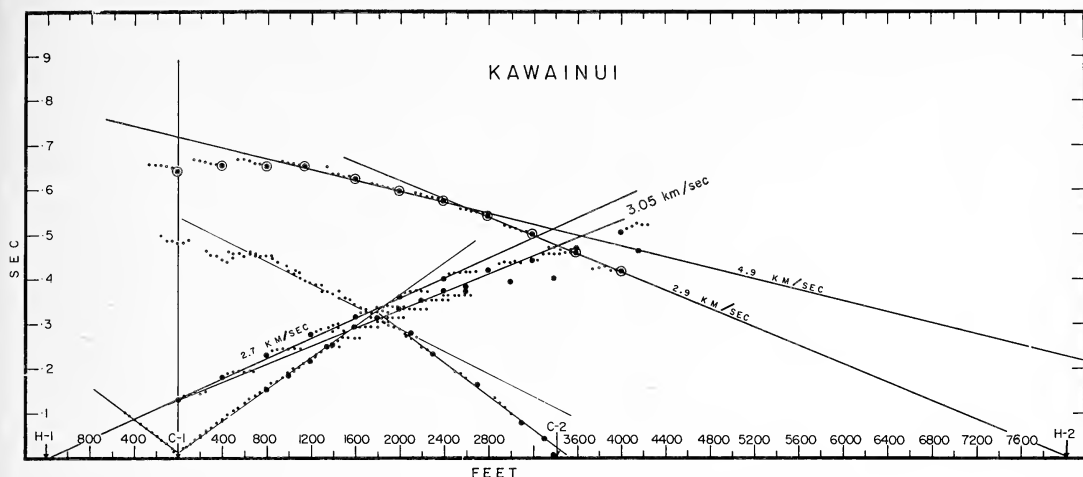


FIG. 4. Travel time plots of refraction traverses in Kawainui Swamp.

and critically examined, corrections for water depth at shot points and elevation at recording sites were made to the raw data.

The corrected data were fed into an IBM 7040 computer for processing. The computer program gave the slopes, velocities, and intercepts of the various branches of the travel-time plots and the variances of the slopes and intercepts. Calculations of depth to the top of the various layers were done by using desk calculators.

#### DATA AND INTERPRETATION

After reviewing the gravity and magnetic data the authors decided to run seismic refraction surveys over the caldera area, the northwest rift zone, and one of the flanks not disturbed by a rift zone. For the flank investigation the western flank was chosen first, but inclement weather forced the transfer of the operations to the southern flank, which is on the leeward side of the island. The short traverses and the GASHOUSE series were designed to outline the volcanic plug in the caldera area; the K-K and ABLE series were planned to parallel as closely as possible the northwest rift zone as outlined by the ridge of high gravity anomalies. The BRAVO series was designed to run along the strike of the south flank. The DELTA series was intended to extend the investigation to the island of Molokai, but data were inadequate to attempt any analysis.

#### Caldera Area

Two consecutive traverses were carried out in the drainage canal which cuts across the northern section of Kawainui Swamp located in the caldera area. For the first traverse recording units were located at C-1 and C-2 of Figure 3 and shots were detonated in the canal at 200-ft or 400-ft intervals. For the second traverse the recording units were placed farther apart at H-1 and H-2, and the shots were again detonated in the canal at 400-ft intervals. The recording units consisted of a 250-ft geophone spread with geophones spaced 50 ft apart. The spread was in line with the shot line.

The travel-time plots for both traverses are shown in Figure 4. The abscissa is given in terms of feet, but the velocities have been converted into units of km/sec for easy comparison with other plots to follow. The larger dots represent the arrival times of the first geophone in the spread. From the figure it can be seen that the apparent velocity across the spread often does not agree with the step-out velocity. This indicates complicated bedding beneath the spread.

A few unusual features are conspicuous on the travel-time plots. For both traverses the plots indicate very high velocities at the ends of the profile. Because the distances involved preclude penetration to great depths, these apparent high velocities have been interpreted in

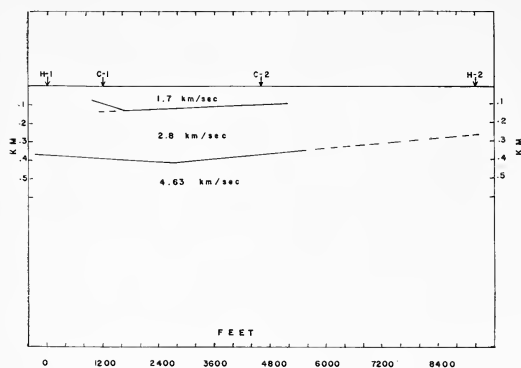


FIG. 5. Section structure under Kawainui Swamp from seismic refraction surveys.

terms of sloping beds, rather than in terms of high-velocity layers. The presence of infinite apparent velocity over the spread at point C-1 gives support to this interpretation.

An interpretation of the travel-time plots and data gave the shallow structure shown in Figure 5. The water layer in the canal (average depth, 4–6 ft) was undetected and hence is disregarded in this discussion because all explosions were set off at the canal bottom. The first layer detected had a seismic velocity of 1.7 km/sec and extended to a depth of 300–400 ft. The second layer had a velocity of 2.8 km/sec. the 2.8 km/sec layer dips  $38^\circ$  under site C-1 to give an apparent infinite velocity across the geophone spread. The third layer, the deepest layer detected, was assigned a velocity of 4.63 km/sec. This value was obtained from the results of GASHOUSE series. The 4.63 km/sec layer dips  $8^\circ$  in the midsection between C-1 and C-2.

For probing the deeper structures in the caldera the GASHOUSE series (Fig. 2) was carried out. Details of the field work, data, and interpretation of this series are given in another paper (Adams and Furumoto, p. 296 in this issue). Analysis showed that a layer of velocity 4.64 km/sec was intruded by a plug that had a velocity of 7 km/sec as a lower bound. The depth to the top of the plug from the ground surface was estimated to be 1.6 km.

#### Northwest Rift Zone

To investigate the northwest rift zone, series ABLE and K-K were carried out. For the K-K

series recording units were placed at Chinaman's Hat Island and at Kailua High School (Fig. 1). The site at Kailua High School is identical with site H-2 described in the discussion on the caldera area. For the ABLE series recording was done at Kahuku and again at Kailua High School (Fig. 1).

The travel-time plots for K-K and ABLE series are given in Figure 6. Notice in the figure that the 5.58 km/sec line is common to the ABLE and K-K series. For the other lines, however, such a happy coincidence does not occur. It is best to consider the two series separately for analysis.

For the K-K series the 5.58 km/sec layer matches the 6.74 km/sec layer in the reversed profile. On the Chinaman's Hat recording a 5.2 km/sec layer is evident and this corresponds to the 4.9 km/sec layer in the Kailua High School recording of the series in the caldera area. However, the pairing of 5.2 and 4.9 should not be done to determine true velocity, because the value of 4.9 is the result of complicated dipping and faulting in the caldera zone. Instead, as was done for the caldera interpretation, the value of 4.64 km/sec, obtained from the GASHOUSE series, was assigned as the true velocity for this layer.

For the layer just below the water the value of 3.0 km/sec was taken from the Chinaman's Hat recording. This layer becomes 2.8 km/sec on land, as was seen in the caldera area data.

Calculations made from the travel-time data yielded the following:

Layer	Velocity (km/sec)	Km to Top of Layer	
		Chinaman's Hat	Kailua
a	3.0	0	0
b	4.64	0.7	0
c	6.1	1.7	0.8

The ABLE series form a reversed profile and a split profile on the northern end. For the Kahuku recording the layer that should correspond to the 5.58 km/sec layer of the Kailua recording is discernible only as second arrivals. The arrivals match well with a set of second and third arrivals with an apparent velocity of 6.8 km/sec on the north side of the Kahuku station.

There is an offset in the Kailua recording of the 7.16 km/sec line. Whether this is due to faulting is not certain.

For the layer just below the water a velocity of 3.0 km/sec has been assigned. This assumption is based on the data from Chinaman's Hat.

Calculations from the travel-time data yielded the following:

Layer	Velocity (km/sec)	Km to Top of Layer	
		Kahuku	Chinaman's Hat
a	3.0	0	0
b	4.17	1.2	0.7
c	5.71	3.8	1.7
d	7.6	5.4	(Dipping 2° to NW)

On the southern portion of the recording at Kailua High School station the velocity of 7.38 km/sec appears as second arrivals. When this value was paired with the 8.17 of the Kahuku

recording, we obtained 7.7 km/sec for layer *d*; 7.7 km/sec was then assigned to layer *d* for the southern portion of the structure.

A section structure for the ABLE and K-K series is given in Figure 7. Notice the consistent lateral variation in velocities; the lower velocities are in the northern section although the layers are deeper.

*The Southern Flank*

For the BRAVO series to the south of the island of Oahu recording units were set up at Barbers Point on Oahu and at Kualapuu on the adjacent island of Molokai (Fig. 1). Distance between the recording units was 109 km. Because of inclement weather, the shots could be set off only in the protected lee of the island of Oahu.

The travel-time plots of the BRAVO series are given in Figure 8. The upper set of lines rep-

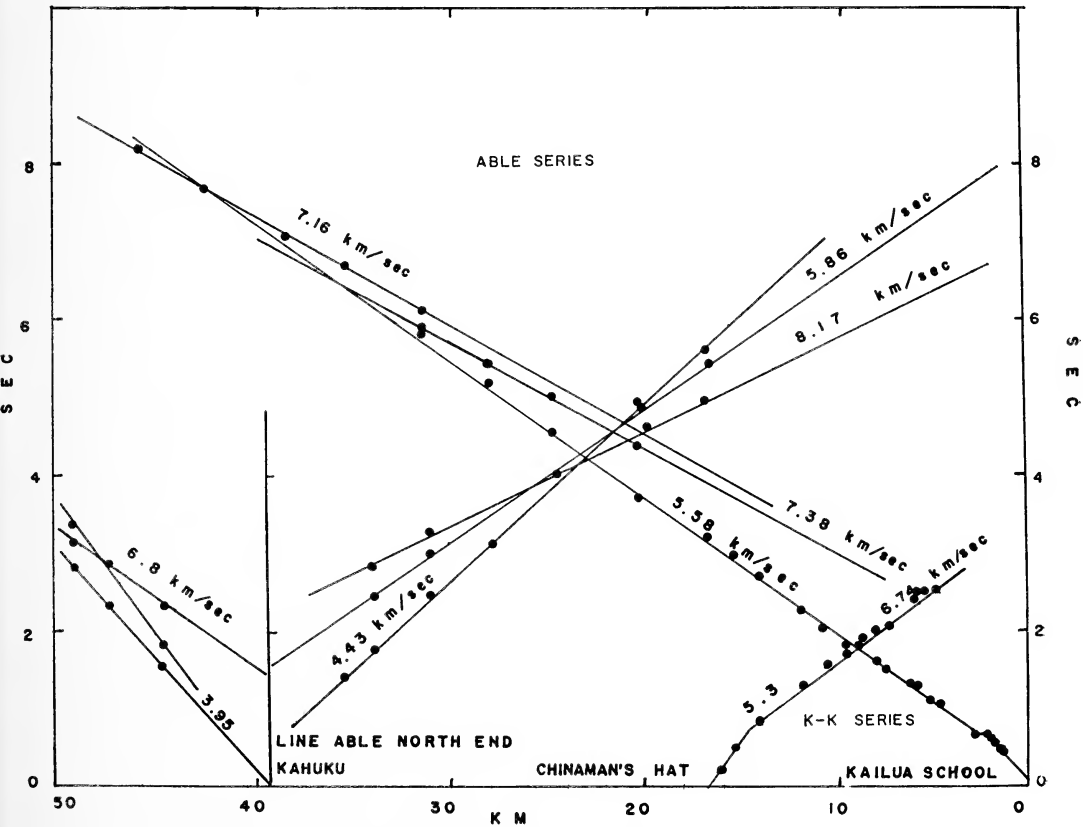


FIG. 6. Travel time plots of K-K and ABLE series.

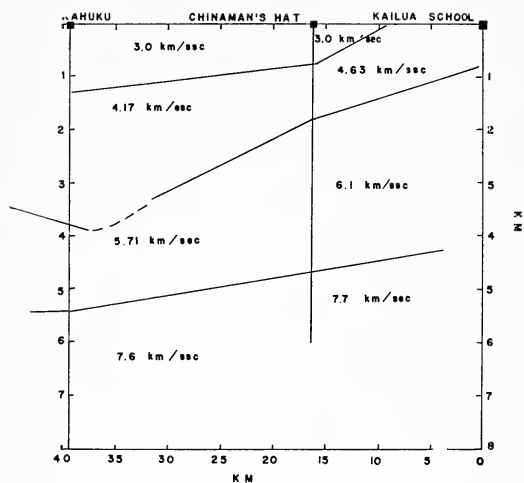


FIG. 7. Section structure under northwest rift zone.

resents the arrival times recorded at Barbers Point; the lower set, the arrival times recorded at Kualapuu.

Because of the shortness of the shot line, interpretation had to rely on second and third arrivals. For these later arrivals correlation from one seismogram to the next was sought by looking for similarity in wave forms as well as linear relations on the travel-time curve.

Interpretation began by assuming that the first layer below the water layer had a velocity of 3.0 km/sec. Then the 4.96 km/sec line of the Kualapuu recording was paired with the 4.97 km/sec line of Barbers Point. The 6.9 km/sec line was paired with the 6.65 km/sec line. The 8.88 km/sec line was considered to be arrivals from the Mohorovicic discontinuity; no comparable line on the Barbers Point recording could be found to match this. The 17.16 km/sec line is probably a reflection from one of the layers.

Inasmuch as the layers with velocities of 4.97 km/sec and 6.8 km/sec showed no dip or very little dip, it was assumed that at least under line BRAVO the Mohorovicic discontinuity was horizontal. This assumption is justified even from gravity data, which showed that the BRAVO series had run along the strike of the flank of the volcano. This assumption results in a velocity of 8.8 km/sec for the mantle.

Calculations from the travel-time data yielded the following:

Layer	Velocity (km/sec)	Km to Top of Layer	Dip
Water	1.5	0	0°
a	3.0	.45 (average)	
b	4.97	2.6	0°
c	6.8	10	1.1°
d	8.8	21	0°

The section structure deduced from the travel-time curves from the BRAVO series is given in Figure 9.

THE STRUCTURE OF KOOLAU VOLCANO FROM COMPOSITE DATA

When the section structures of the caldera, northwest rift zone, and southern flank were fitted together, the over-all structure of Koolau Volcano shown in Figure 10 was obtained.

Three layers were detected in the northwest rift zone. The unusual feature of a high velocity layer, 7.6–7.7 km/sec, at very shallow depths, should be noted.

An explanation of this phenomenon is that differentiation in the magma chamber under the rift zone separated the magma into a 5.7–6.1 km/sec layer and a 7.6–7.7 km/sec layer. Further investigation with longer refraction traverses should be carried out over the rift zone to determine whether there is another layer with higher velocity under the 7.6–7.7 km/sec layer.

From interpretations of the reflected phase of the GASHOUSE series, Adams and Furumoto (p. 296 in this issue) proposed a magma chamber at a depth between 3 and 4 km. This agrees well with the depth to the 7.6–7.7 km/sec layer which, when extended to the cal-

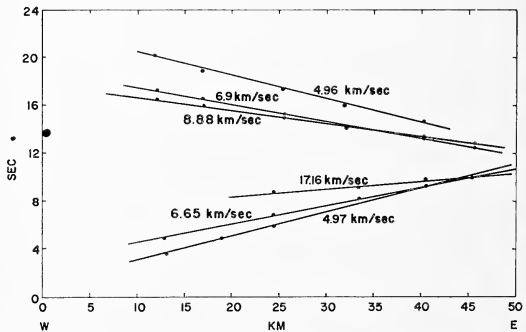


FIG. 8. Travel time plots of BRAVO series.

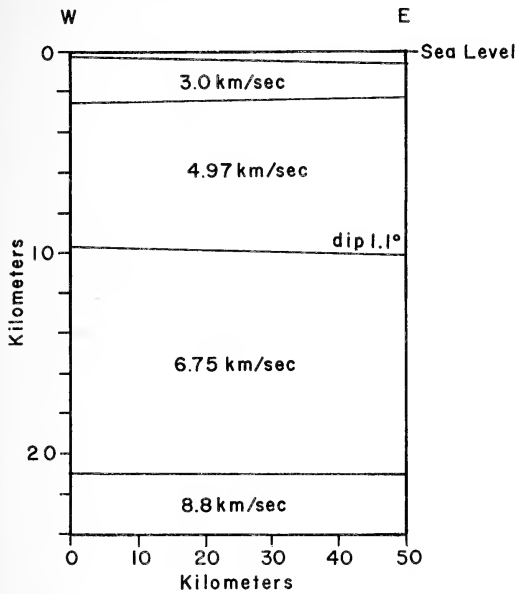


FIG. 9. Section structure on south flank.

dera area, attains a shallow depth of about 4.3 km.

The behavior of the 5.7–6.1 km/sec layer is curious, because it appears clearly in the K-K series but was undetected in the GASHOUSE series. Hence, we have the interpretation that this layer pinches out at the north end of the plug.

The section structures from BRAVO series and GASHOUSE series have been juxtaposed for the southern flank. Because of the disparate character of the two, the grounds for juxtapositioning may not be as firm as those for the rift zone and the plug; but the composite picture fits well with the gravity survey (Strange, Woollard, and Rose, p. 381 in this issue). The depth of 21 km for the Mohorovicic discontinuity for the southern flank is deeper than normal for oceanic areas, but far from startling for volcanic islands. The results of refraction surveys by the U.S. Geological Survey show that along

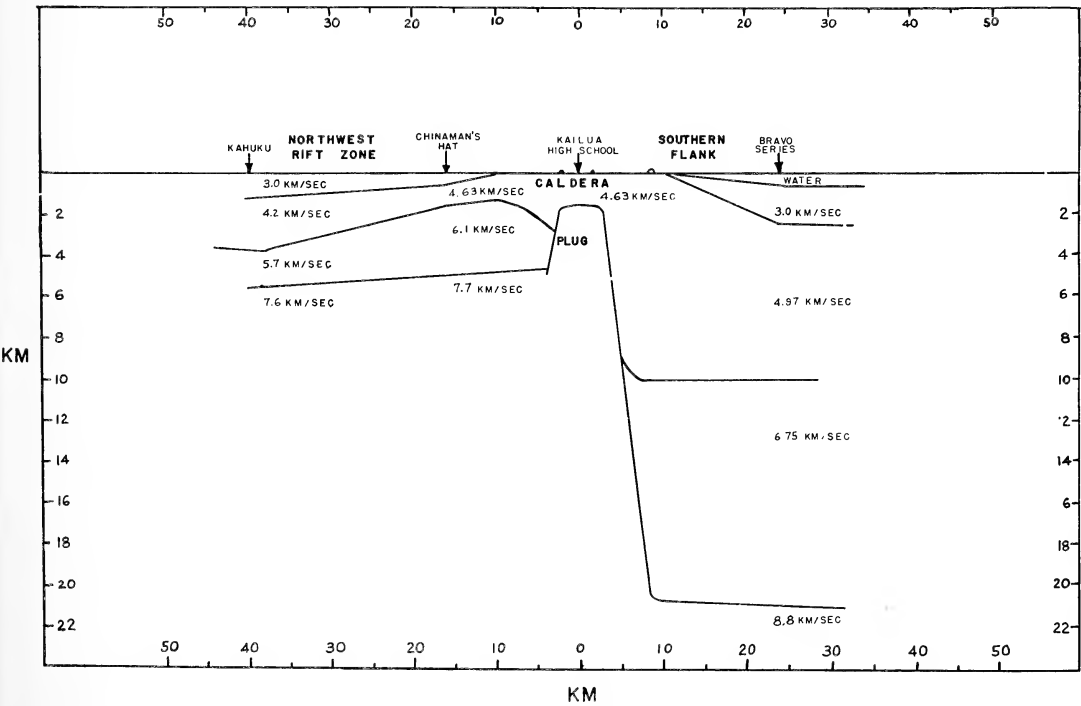


FIG. 10. Section structure of Koolau Volcano from composite seismic refraction data.



the western shore of the island of Hawaii the Mohorovicic discontinuity is at a depth of about 16 km (D. Hill, 1964, personal communication).

An interesting product of the study is the existence of high velocity materials at shallow depths in the rift zone and in the plug of the volcano. The value of 7.7 km/sec is close to the arbitrary value of 7.8 km/sec assigned to mantle material. It can be conjectured that mantle material has risen through the plug and rift zone to shallow places. It can also be postulated that differentiation in magma chambers caused denser material with higher seismic velocity to settle out. But all these are conjectures which can be resolved only by analysis of actual samples obtained by drilling in the rift zone and plug, or by drilling to depths considered to be the normal mantle.

#### CONCLUSIONS AND ACKNOWLEDGMENTS

The seismic refraction project carried out over the Koolau Volcano yielded an over-all picture of the subsurface structure that fits well with gravity and magnetic data. Materials of unusually high velocity at shallow depths were found in the plug and rift zone. This may very well be the first time that quantitative values for the internal structure of a volcano have ever been published.

Further investigations by seismic techniques

are recommended, especially on the eastern flank and the southeast rift zone.

The authors thank the numerous staff members and graduate students of the Hawaii Institute of Geophysics who participated in carrying out the difficult field work of the project.

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# Seismic Refraction Studies of the Crustal Structure of the Hawaiian Archipelago<sup>1</sup>

AUGUSTINE S. FURUMOTO and GEORGE P. WOOLLARD

IN RECENT YEARS several seismic refraction studies have been made of the crustal structure in and near the Hawaiian Islands. Earlier investigators were Raitt (1956) and Shor (1960). A crustal analysis of earthquake travel time was made by Eaton (1962). Shor and Pollard (1964) made refraction studies to the north of the island of Maui in connection with Mohole site selection investigations. Results of recent refraction studies over the Koolau volcano on the island of Oahu are reported in other papers in this issue (Furumoto et al., p. 306; Adams and Furumoto, p. 296). Some unpublished results include those from the seismic refraction survey made in 1963 by Western Geophysical Company, over the area as outlined by Shor and Pollard, that showed a subnormal depth to the mantle, and from the refraction surveys conducted by the U.S. Geological Survey across the island of Hawaii during the summers of 1963 and 1964. Of these, the authors had access to the results obtained by Western Geophysical Company and, through verbal communication with D. Hill, to those of the Geological Survey.

Because seismic results can best be considered in terms of their location, they will be divided on the basis of their geomorphic associations. Three crustal and geomorphic provinces are represented: the Hawaiian Arch, the Hawaiian Deep, and the Hawaiian Ridge. The locations of the measurements relative to these three features are shown in Figure 1, along with depth to bottom and depth to mantle. The recording stations of the refraction surveys are designated by numbers or letters in Figure 1. Two numbers are listed next to the station designation; the upper number gives the depth to the ocean bottom, and the lower the depth to the Moho discontinuity.

## THE HAWAIIAN ARCH

The Hawaiian Arch is a broad topographic feature lying to the north of the Hawaiian Ridge and separated from it by the north Hawaiian Deep or Trench.

Shor and Pollard (1964) found that over the Hawaiian Arch the average depth to the Moho is 10.4 km. At one location (Station 29 of Fig. 1) the depth to the Moho was as shallow as 9 km. These workers claim an accuracy of  $\pm 0.5$  km for their depth estimates. The repeat studies in the same area by Western Geophysical Company and a reanalysis of Shor and Pollard's data by the National Science Foundation confirm these results in general. The new data and the reanalysis show that the average depth to the mantle in this area is 10 km. The structure of the crust in the area is defined by four distinct layers having the following velocity values: Layer *a*, 2.15 km/sec; layer *b*, 4.20 km/sec; layer *c*, 5.56–6.41 km/sec; layer *d*, 6.82–7.01 km/sec.

The underlying mantle has a velocity of 7.97–8.68 km/sec, which appears to vary according to azimuth. East–west oriented measurements have a higher velocity than those oriented north–south. This suggestion of anisotropy is definitely established in one section where cross-oriented measurements show a velocity of 8.1 km/sec in a north–south direction, and of 8.7 km/sec in an east–west direction. As all the measurements were reversed to obtain true velocity values, anisotropy appears to be well established. On the basis of the combined studies of the Western Geophysical Company and Shor and Pollard, a site for a potential drill hole to the mantle was designated at approximately 22°22'N and 155°28'W. The site, as seen in Figure 1, lies on the southern flank of the Hawaiian Arch at a location where the depth of water is about 2380 fathoms (4350

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 91.

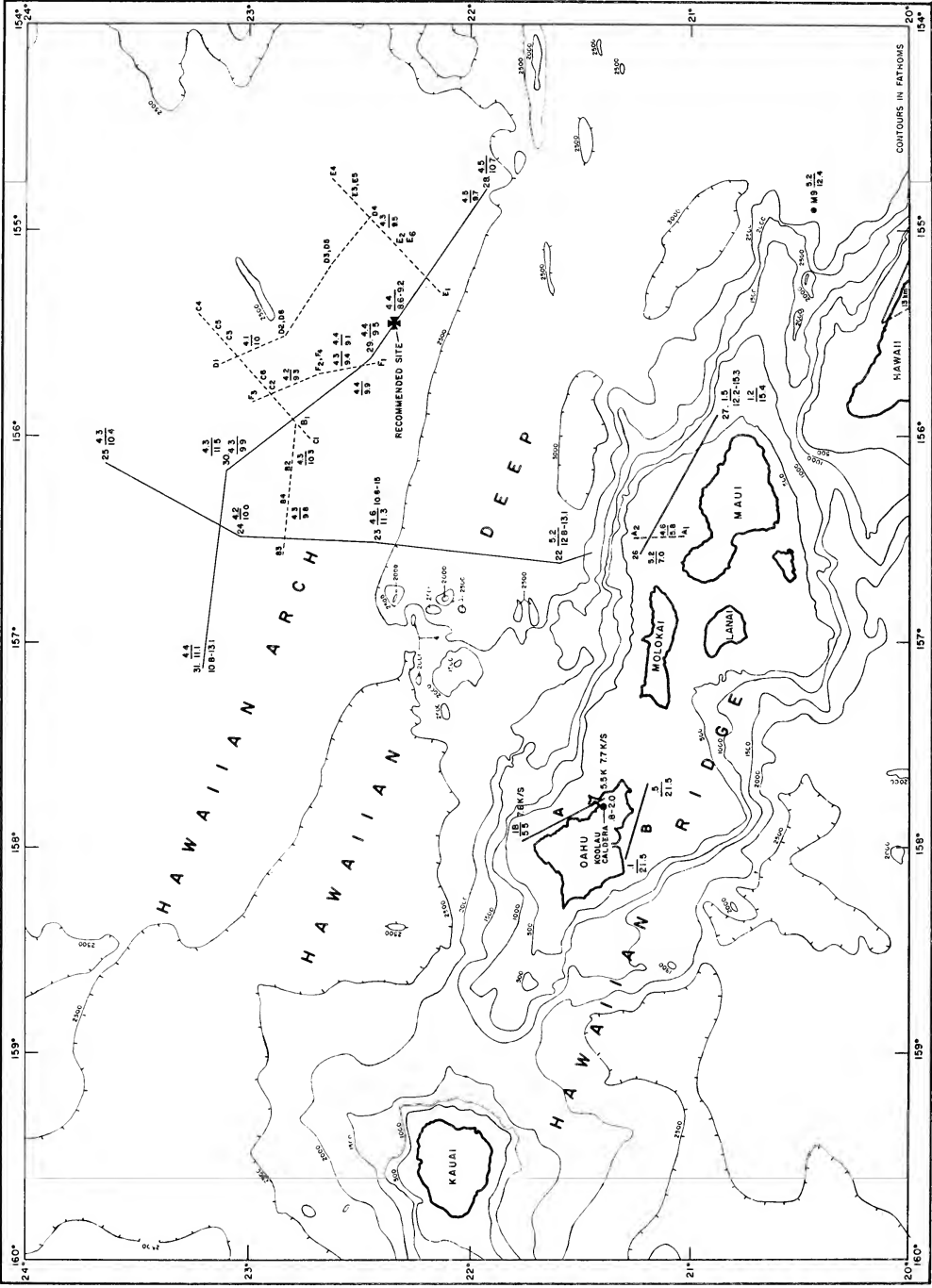


FIG. 1. Location of seismic measurements and depths to mantle.

m). The estimated depth to the mantle is  $9 \pm 0.4$  km. This location corresponds roughly with Shor and Pollard's Station 29, where they obtained what appeared to be anomalous crustal structure. Here their measurements indicate that the basal crustal layer has a velocity of 6.97 km/sec, which is somewhat high for this layer, and that the layer's thickness is only about half its normal value. However, the reanalysis of their data by the National Science Foundation, as shown in Figure 2, indicates much less abnormality in crustal thickness and much less variation in adjacent depths to the mantle. As seen in Figure 2 the average mantle depth is 10 km.

THE HAWAIIAN DEEP

Shor and Pollard (1964) established one pro-

file over the Hawaiian Deep (Station 22, Fig. 1) and found that the mantle there was deeper than normal, 13 km. The overlying crust is composed of four layers having velocity values similar to those observed on the Arch. Although layer *c* is relatively thin, layer *d* is significantly thicker than elsewhere. An earlier measurement on the flank of the trench off the east coast of Hawaii by Raitt (1956) showed a crust composed of three layers with a depth to the mantle of 12.4 km.

THE HAWAIIAN RIDGE

Shor and Pollard (1964) established one profile (Station 26, Fig. 1) on the shallow water shelf just north of the island of Maui that is of considerable interest. The Moho discontinuity,

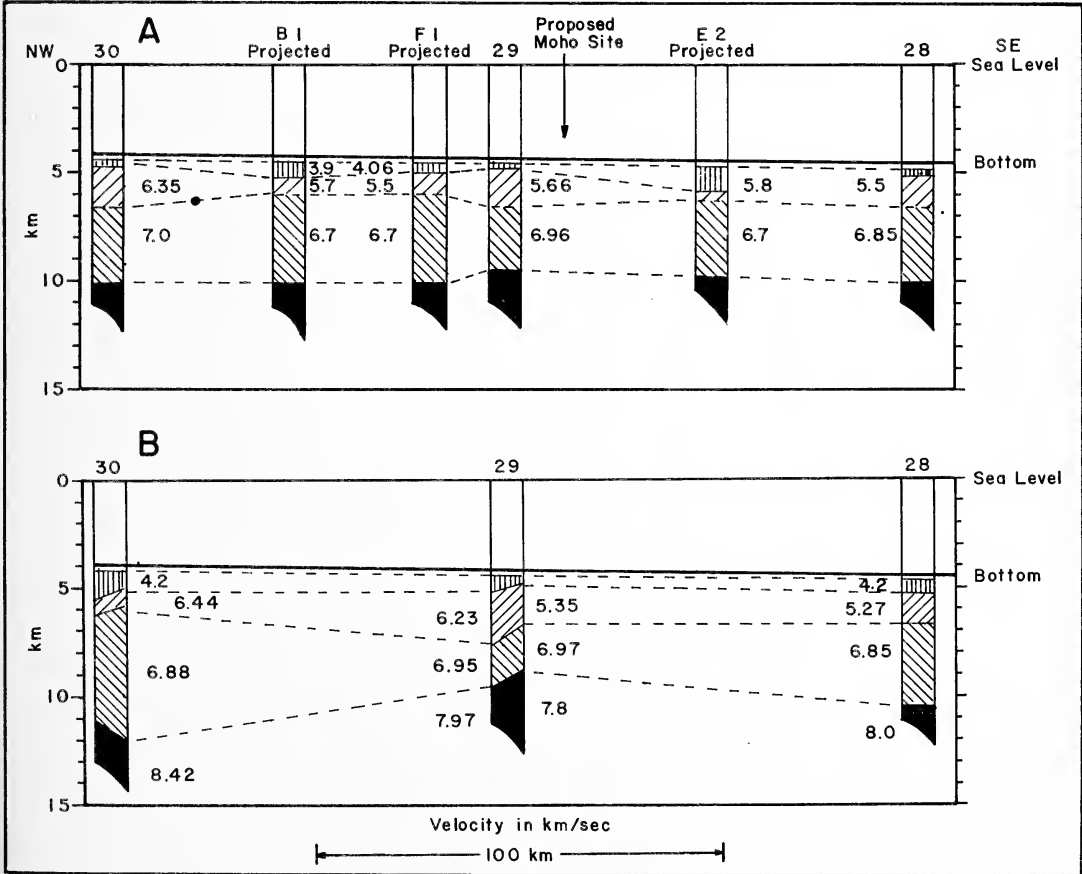


FIG. 2. A: NSF reworked crustal section across proposed mohole site. Stations 28, 29, 30 after Shor and Pollard (1964); stations B1, F1, E2 from unpublished data of Western Geophysical Co. B: Published section (after Shor and Pollard, 1964) along northwest-southeast section on flank of Hawaiian Arch.

having a velocity of 8.10 km/sec, showed irregularities in depth which they felt appeared to be best explained by faulting, the upthrown side of the fault giving an anomalous depth to the mantle of 7 km. This, however, could be related equally as well to a buried volcanic rift or pipe filled with mantle-like material. The magnetic relations (Malahoff and Woollard, in a forthcoming issue of *Pacific Science*) strongly suggest this as the true explanation. The reality of very shallow mantle material here is substantiated by the Western Geophysical Company measurements which yielded a depth of 5–8 km in the adjacent area (Station A1-A2, Fig. 1).

Another shelf section off the east end of Maui, examined by Shor and Pollard (Station 27, Fig. 1), showed a depth of 15.5 km to the mantle, with a crust having the following velocity structure: Layer *a*, 2.68 km/sec; layer *b*, 3.65 km/sec; layer *c*, 4.96 km/sec; layer *d*, 7.15 km/sec(?); Moho, 8.10 km/sec.

Layer *d* was not actually defined, but probably is present. The results obtained along the north coast of Hawaii by the U.S. Geological Survey, recording on land and shooting at sea (Eaton and Ryall, personal communication), suggest a depth to the mantle of 13.0 km in this area. This agrees with the analysis made by Eaton (1962) of earthquake travel time data on Hawaii, which suggested a depth of 13–15 km to the mantle.

The work of the Hawaii Institute of Geophysics was concentrated in and around the island of Oahu and was concerned with both crustal structure and centers of volcanic eruption. Detailed explanation and results are given elsewhere in this issue (Furumoto et al., p. 306; Adams and Furumoto, p. 296). In brief, these studies showed Moho-like velocities at very shallow depths (1–2 km) over primary volcanic pipes and at deeper depths (6 km) beneath the rift zones. The volcanic pipe measurement, showing a velocity greater than 7.0

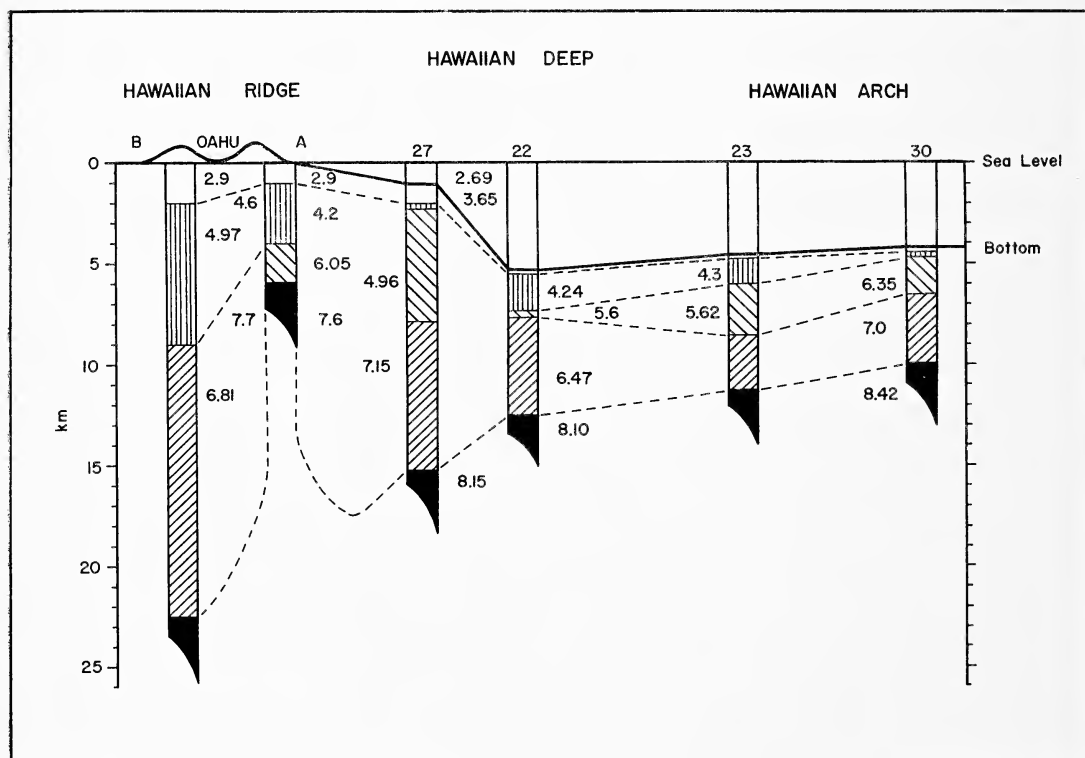


FIG. 3. Composite crustal section across the Hawaiian Archipelago. Stations A and B after Furumoto et al. (p. 306 in this issue); stations 27, 22, 23, 30 after Shor and Pollard (1964). Velocity in km/sec.

km/sec, was made over a plug in the caldera area of Koolau Volcano. The plug had intruded into a layer having a velocity of 4.63 km/sec. The rift zone measurement, showing a velocity of 7.6–7.7 km/sec, was made on a profile paralleling the northwest rift zone of the Koolau Volcano. The northwest rift zone was outlined by a local gravity anomaly high (+50 mgal) which indicates an abnormal mass distribution.

It is not clear whether the 7.6–7.7 km/sec layer which occurs at a depth of about 5.5 km under the rift zone is the true mantle or, more likely, is a differentiate of the mantle marking the magma chamber that furnished the Koolau Mountain volcanics.

To the south of Oahu a crustal traverse, although with incomplete measurements, indicated mantle depth to be close to 21 km. If the same slope associated with the basal crustal layer's upper surface applies to the crust-mantle interface, the mantle velocity is at least 8.4 km/sec.

It should be mentioned that the occurrence of intrusive bodies, such as the plug in the caldera, complicates refraction measurements on volcanic islands. The relatively small area of the islands, precluding long refraction spreads on land, imposes another complication. Therefore, it is not surprising that the present measurements, incomplete as they are, are the first to come up with values on the depth to the mantle. Previous studies of volcanic islands, such as those made by Officer et al. (1952) on Bermuda, by Raitt (1952) on Kwajalein and Bikini, and by Gaskell and Swallow (1953) on Funafuti and Nukufetau, have defined only the depth to the volcanics and, in a few cases, to the upper crustal structure. All failed to give information on crustal thickness or to define the seismic nature and boundaries of the volcanic pipes and rift zones present.

#### SUMMARY

On the Hawaiian Arch the depth to the mantle is about 10.0 km on the average and locally is as shallow as 9 km. On the shelf area north of Maui a velocity comparable to the velocity of the Moho is found at a depth of 5.8 km. Magnetic data suggest this shallow depth is re-

lated to an intrusive. On the island of Oahu high velocity material of 7.7 km/sec is also found at a shallow depth (5 km). This is related to a known volcanic rift zone marked by high gravity and magnetic values. South of Oahu along the axis of the Hawaiian Ridge a depth of 20–23 km is defined for the mantle. Between the Hawaiian Ridge and the Hawaiian Arch in the area of the Hawaiian Deep the depth to the mantle is about 13.0 km. The above relations are summarized by a composite section across these three features, as shown in Figure 3. This section shows clearly that the origin of the Hawaiian Deep must be related to crustal subsidence beneath the Hawaiian Ridge. This is in agreement with current theory on the origin of seamounts and atolls, and would explain the progressive change from atolls at one end of the Hawaiian Ridge (Midway I.) to the high relief (13,500 ft) associated with Hawaii on the other end of the Ridge.

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# Hawaiian Calderas<sup>1</sup>

GORDON A. MACDONALD

**ABSTRACT:** Hawaiian calderas form by collapse during the last stages of growth of shield volcanoes built by frequent eruptions of tholeiitic basalt. They range from 2–12 miles across, have sunk several thousand feet, and in part have grown piecemeal by coalescence of smaller collapse craters. They may never have formed on some volcanoes, and all are partly or wholly filled by continued eruption. Toward the end of the filling activity slows, and alkalic lavas complete the filling and build a thin cap over the caldera.

Gravity studies reveal masses of ultra-dense rocks only 1–2 km below the surface of several of the volcanoes—perhaps olivine-rich cumulates in the feeding pipe of the volcano, or perhaps protrusions of the mantle. The idea that these may have led to formation of the calderas by isostatic sinking of a heavy column culminating in the caldera appears to be negated by the facts that some calderas show no associated gravity high, in some the high is offset to one side of the caldera, and some highs are not associated with any apparent caldera collapse.

Caldera formation probably depends on the formation of a magma reservoir within the mass of the shield volcano, with its top within a few kilometers of the summit of the shield. The Glen Coe mechanism of caldera formation seems to be ruled out by the lack of upward displacement of magma around the sinking block. Caldera collapse is probably the result of sinking of a block bounded by inward-dipping conical fractures, permitted by distension of the top of the volcano and removal of support due to drainage of magma into the rift zones, with or without flank eruption. The distension of both the summit region and the rift zones may result from a lateral spreading of the lower part of the ultra-dense core of the volcano.

THE ORIGIN OF HAWAIIAN CALDERAS has been discussed several times before (Stearns and Clark, 1930; Stearns and Macdonald, 1946; Macdonald, 1956), but with the increase in knowledge of the physical properties of Hawaiian rocks and magmas and the geophysics of Hawaiian volcanoes during the last decade it is desirable to review the former conclusions, to see whether they need modification. It may be assumed as a starting point that the calderas are formed by collapse. They obviously are not formed by erosion, and the very small amount of pyroclastic debris at and near the summits of the shields clearly eliminates any possibility of their having been blasted out by explosion. There is general agreement that they have been

formed by the sinking in of the summit regions of the shield volcanoes. The term "volcanic sink" used for them by R. A. Daly (1914:144–147) is an appropriate one, though it has not been widely used, at least partly because of potential confusion with other types of geologic "sinks."

Though the generality of the collapse origin of Hawaiian calderas is unquestioned, the cause of the sinking is still uncertain. The purpose of this paper is to describe briefly the calderas, to sketch their spatial and time relationships to the volcanic structures and history, to reexamine the suggested causes of collapse, and to suggest a new mechanism that may be of importance in bringing about the distension of the mountain that is indicated both by the sinking of the caldera and by the rift zones.

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 92.

## MORPHOLOGY OF THE CALDERAS

The summits of the active shield volcanoes, Kilauea and Mauna Loa, are indented by oval calderas. That of Kilauea is 4.4 km long and 3 km wide. Mokuaweoweo caldera, at the summit of Mauna Loa, is 4.5 km long and 2.6 km wide. Both are slightly excentric with respect to the precise summits of the mountains. Kilauea caldera is 150 m deep at its western edge, beneath the highest point of the mountain, but its walls decrease in height essentially to zero at its south side. It is separated from the adjacent pit crater of Kilauea Iki by only a low, narrow ridge (the Byron Ledge). Mokuaweoweo is 180 m deep at its western edge, 130 m deep at its eastern edge. At the south it merges with the pit crater, South Pit, and at the north its floor is continuous into the pit crater known as North Bay, which is bounded at the north by a wall only about 5 m high. At its northeast edge Mokuaweoweo also merges with the very small pit crater, East Bay; and farther north the pit crater Lua Poholu lies within the outermost faults of the caldera. It is generally agreed that the pit craters, like the calderas, have formed by collapse.

Extending outward from the calderas are the rift zones of the volcanoes (zones of fracturing averaging about 3 km wide) that have served as the feeding conduits for most flank eruptions of the volcanoes. On the southwest rift zone of Mauna Loa, within 3 km of Mokuaweoweo, lie three pit craters, the central one of which has been formed since 1840. Along the east rift zone of Kilauea within 20 km of the caldera lies a whole series of pit craters (Stearns and Macdonald, 1946: Pl. 1).

In most places the boundaries of the calderas are steep cliffs, with an average slope of about 75°. Layers of lava in the cliffs slope outward away from the summit of the mountain and their truncated edges project upward into space in the present area of the depression. The vents that fed them must have been located at a higher level, and must have dropped out of sight at the time of origin of the caldera. In other words, the caldera cannot have been present in anything approaching its present dimensions until the shield had reached essentially its

present size. The cliffs bounding the calderas are fault scarps. Along most of the boundary the cliff is simple, but in places it consists of a series of step-fault blocks. The fault planes separating the step blocks appear to dip toward the center of the caldera at about the same angle as the rest of the boundary scarp. Locally, the faults pass into monoclines (Macdonald, 1957).

The main calderas are partly surrounded by benches as much as 3 km wide that have also been dropped down on faults, but not as far as the central caldera. Viewed from an airplane a short distance away, the summit areas of both Kilauea and Mauna Loa are seen to have sagged downward over a subcircular area 6–8 km across, with the sharply defined downfaulted calderas at the center.

The floor of Kilauea caldera is a very gently sloping dome or cone rising to an apex at Halemaumau crater, in the southwestern part of the caldera. The cone was formed by repeated overflows from Halemaumau during the long period of lava lake activity before 1924, with the minor addition of the lava flow of the 1954 eruption (Macdonald and Eaton, 1957). The floor of Mokuaweoweo also slopes upward toward the cones of the 1940 and 1949 eruptions. During the last 150 years the history of the calderas has been one of repeated collapse of the floor and refilling by eruptions on the floors. In 1825 the center of Kilauea caldera was a pit some 260 m deep, surrounded by a narrow "black ledge" 30 m or so below the present floor level. This central depression is presumed to have formed by collapse at the time of the flank eruption in 1823. By 1832 the central pit had been filled to overflowing, but in that year it was reestablished in much its former condition by another collapse. Again it was refilled, only to be reformed by collapse accompanying the eruption of 1840. Still again it was refilled, only to sag down in a less extensive depression at the time of the 1868 eruptions, and so on. From 1840 onward each collapse was smaller than the one that preceded it, until in the 1920's two small collapses were followed by a large one (Table 1). It should be noted here that the collapses of the 19th century listed in the table represent the volume



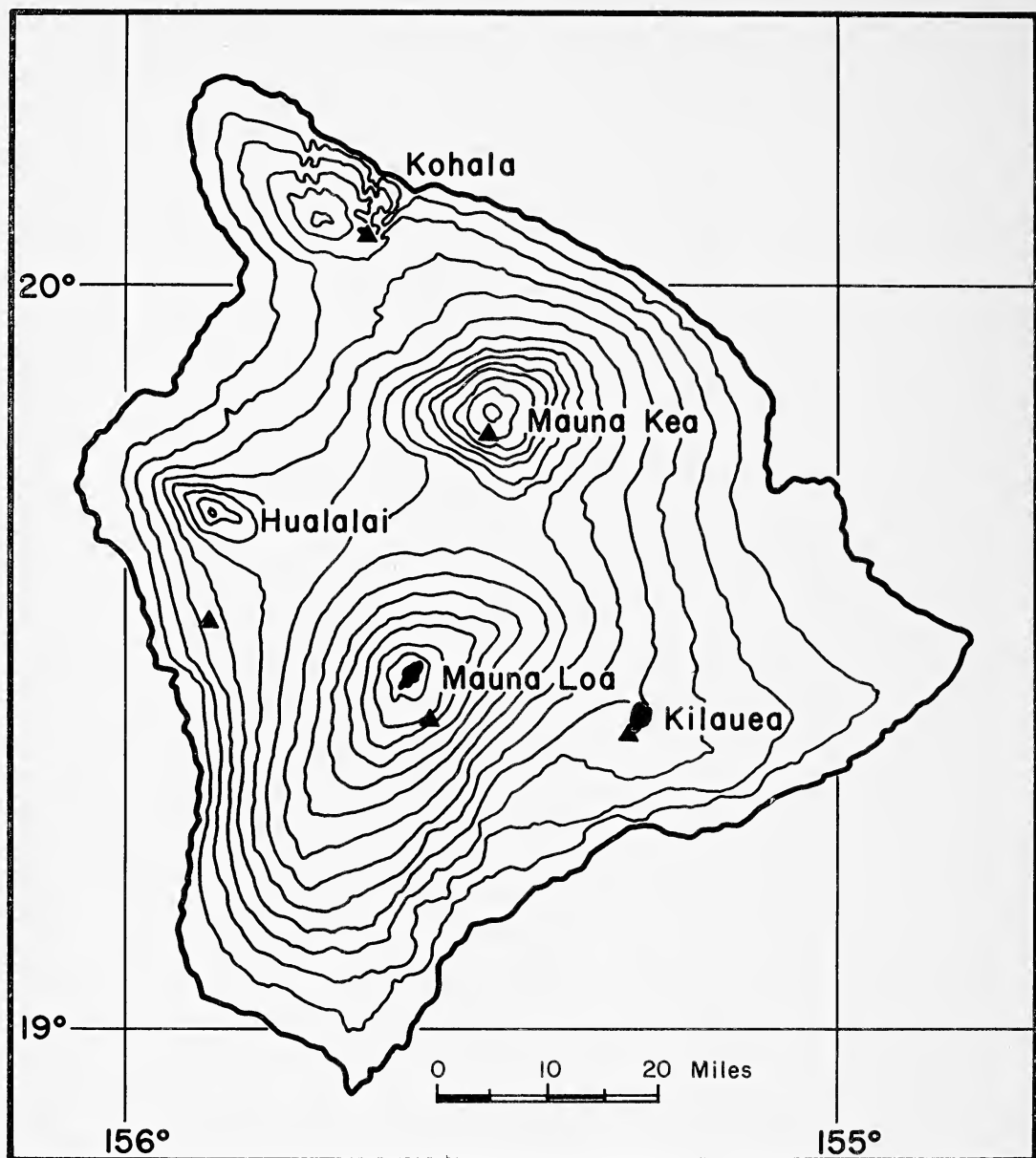


FIG. 1. Map of the island of Hawaii, showing the locations of the major volcanoes, the calderas (*solid black spots*), and the approximate centers of the gravity highs (*black triangles*) as located by Kinoshita et al. (1963).

of the sharply defined central depression only, whereas those of 1924 and 1955 include the volume of a gentle sinking of the mountaintop that could not have been detected without sensitive tiltmeters or precise surveying, so that actually the early collapses must have been somewhat larger in relation to the later ones than is indicated by the table.

The history of Mokuaweoweo is known in far less detail. A large collapse of the caldera floor in the middle part of the 19th century may have been associated with one, or possibly more than one, of the flank eruptions of Mauna Loa. Since then the depression has been gradually refilled, until in 1949 lava poured out of the caldera into South Pit, filled it to over-

flowing, and continued for several kilometers down the mountainside. Until 1948 a crescentic bench (the South Lunate Platform) remained around the south side of the central pit, but it has been largely buried by the lavas and cones of the 1949 eruption.

The original morphological forms of the calderas of the older Hawaiian volcanoes have been wholly destroyed by erosion, but the calderas are nevertheless clearly delineated by mapping. The lavas that filled the calderas are thick-bedded, generally moderately to very dense, and essentially horizontal, in contrast to the thin-bedded moderately to highly vesicular flows that accumulated with slopes of 2–10° on the flanks of the volcano outside the caldera. The thickness and horizontality of the caldera-filling flows resulted from their being confined within the caldera depression, and their dense-

ness resulted from the greater proportion of gas that was able to bubble out of the thicker flows before they solidified. The contrast in general aspect and attitude of the two groups of flows is usually sufficient to indicate the former position of the edge of the caldera. In addition, banks of talus commonly formed against the foot of the caldera-boundary cliffs, as they are doing in Kilauea and Mauna Loa calderas today. The lavas accumulating within the caldera buried these taluses, and later erosion has exposed them as prisms of breccia between the caldera-filling and extra-caldera lavas. Careful mapping by H. T. Stearns has delineated the calderas of the Koolau and Waianae volcanoes on Oahu, and those on east Molokai, West Maui, and the exposed end of that of Kahoolawe. The caldera of the Koolau volcano was about 8 km long and 5 km wide, cen-

TABLE 1  
VOLUMES OF CALDERA COLLAPSE COMPARED WITH VOLUMES OF FLANK LAVA FLOWS  
AT KILAUEA VOLCANO DURING HISTORICAL TIMES

YEAR	VOLUME OF COLLAPSE (m³)	VOLUME OF FLANK LAVA FLOWS (m³)	
		Actual	Reduced to approximate volume in magma chamber
1823	539,500,000	14,000,000 <sup>a</sup>	11,200,000
1932	580,600,000	?	.....
1840	219,500,000	214,800,000 <sup>b</sup>	171,800,000
1868	188,300,000	< 5,000,000	< 4,000,000
1886	39,600,000	?	.....
1891	34,000,000	?	.....
1894	8,500,000	?	.....
1916	8,300,000	0	0
1919	10,000,000	73,800,000 <sup>c</sup>	59,000,000 <sup>c</sup>
1922	21,200,000	8,700,000 <sup>d</sup>	7,000,000
1924	201,600,000	0	0
1950		0	0
1955	200,000,000	141,000,000	113,000,000

<sup>a</sup> Includes an estimated 2,000,000 m³ that poured into the ocean.  
<sup>b</sup> Includes an estimated 150,000,000 m³ that flowed into the ocean.  
<sup>c</sup> Includes the volume of the flow in the caldera in 1919 and the flow on the southwest rift zone in 1919 and 1920.  
<sup>d</sup> Includes the volumes of flows on the caldera floor in 1921 and on the east rift zone in 1922.

tering at the Kawainui Swamp near Kailua (Stearns, 1939: Pl. 1). That of east Molokai was about 7.2 km long and 5 km wide (Stearns, and Macdonald, 1947:19, Pl. 1). The largest of the Hawaiian calderas was that of Kauai, some 16 by 20 km across (Stearns, 1946: Fig. 22; Macdonald, Davis, and Cox, 1960: Pl. 1). In and close to the east Molokai and Koolau calderas, and locally in that of West Maui and near the boundary of that of Kauai, rising gases brought about chloritization of the rocks and deposited secondary minerals, including quartz and chalcedony. The boundary cliffs of the calderas, as delineated by mapping, sloped inward at angles of  $50^\circ$  to nearly  $90^\circ$ , averaging about  $75^\circ$ . The slope of the boundary cliffs is not, of course, necessarily the same as that of the faults that bound the sunken block at depth. Outward-dipping faults would produce surficial scarps that are unstable, and slumping would quickly form inward-sloping fault-line scarps. However, other evidence discussed on a later page also suggests that the subsurface faults dip inward.

Nowhere has the bottom of the caldera-filling mass been reached by erosion. The sinking of the original tops of the east Molokai and Kauai shields exceeded 1,400 m.

There is considerable evidence that Mokuaweoweo caldera grew in part by the repeated inclusion of marginal pit craters (Stearns and Clark, 1930:49; Stearns and Macdonald, 1946: 29). On the floor of Kilauea caldera also, the distribution of areas of alteration of the rocks by rising gases indicates the presence of a series of pits buried by the lavas erupted within the last 150 years (Macdonald, 1955a). The Kilauea Iki and Keanakakoi pit craters nearly coalesce with the inner caldera of Kilauea, and the outermost caldera faults are beyond them, so that they are actually within the major sunken area. The pit craters probably have formed by sinking of a roof block into an underlying magma chamber eaten upward into the mass of the volcano by stoping and melting of the lavas above the magma body (Macdonald, 1956:281), but since the sinking is not accompanied by a rise of magma along the bounding ring fractures into the crater the magma must have been withdrawn, into adja-

cent rift fractures or elsewhere, to make room for the sinking block.

#### RELATION OF CALDERA FORMATION TO VOLCANIC AND MAGMATIC HISTORY

As a result of his years of study of the areal geology of the Hawaiian Islands, H. T. Stearns was able to distinguish a series of stages in the history of the volcanoes (Stearns, 1940; 1946: 17-19). These may be summarized briefly as follows, with some additions and modifications from Stearns' original statements:

1. A youthful shield-building stage, during which frequent eruptions of very fluid basaltic lava build a shield volcano composed almost wholly of thin extensive lava flows. Eruptions come so frequently that there is not time for any appreciable amount of weathering or erosion between successive flows. Pyroclastic material forms probably less than 1% of the part of the shield above sea level. Hydromagmatic explosions may have produced a much larger proportion of pyroclastics in the zone within a few hundred feet below sea level, but at greater depths the pressure of overlying water probably effectively restrained both explosion and vesiculation, and the lava flows were probably much denser than those later poured out above sea level, as are those formed in deep water on the east rift zone of Kilauea (Moore, 1965).

2. Late in the period of shield building the summit of the shield collapsed to form the caldera. There followed the so-called caldera-filling period, during which thick massive lava flows accumulated within the caldera, gradually filling it. It should be noted, however, that eruption is not restricted to the caldera, but continues to take place on the flanks of the volcano also, and the shield continues to build. Volcanism continues vigorous and eruptions frequent; the activity remains almost purely effusive and pyroclastic material still is formed in only very small amount.

3. Eventually the caldera becomes filled and the volcano enters on the post-caldera, or old-age, stage. Eruptions become less frequent, and many of them are more explosive, partly because of greater viscosity of the erupting magma but partly also because of a greater abundance

of gas. Local erosional unconformities, stream gravels, and soil beds are found between successive flows, and the proportion of pyroclastic material increases. The spatter cones built by Hawaiian-type eruptions characteristic of the shield-building stage are largely replaced by cinder cones built by strombolian-type eruptions. A relatively thin cap, a few tens to several hundreds of meters thick, is built over the top of the shield and the filled caldera.

4. Extinction of the major volcano is followed by a long period of volcanic quiescence, with deep erosion and weathering. Sea cliffs several hundred meters high and canyons several hundred meters deep are cut into the volcanic mountain.

5. At some volcanoes (whether eventually at all is unknown) volcanic activity returns. In this rejuvenated, or post-erosional, stage new eruptions take place from rift zones that have little or no relationship in position or direction to those of the earlier stages. Lava flows partly fill valleys and relatively small lava, cinder, and tuff cones are built against the dissected surface of the old mountain, separated from it by a profound erosional unconformity and sometimes by intervening sedimentary deposits such as coral reefs.

It should be noted that not all Hawaiian volcanoes have passed through all of the above stages. Lanai appears to have stopped activity at about the end of the caldera-filling stage. Kilauea and Mauna Loa are still in the caldera-filling stage and Hualalai appears to have barely entered the old-age stage. Neither Hualalai nor west Molokai now has any caldera, nor do they show any indication of ever having had one, though on both a caldera may have been hidden by later flows. On Mauna Kea the suggestion of a former caldera is very tenuous, consisting only in an arcuate arrangement of some of the cinder cones in the summit region that may reflect caldera-related ring fractures at depth (Macdonald, 1945). These volcanoes may have skipped the caldera-forming and caldera-filling stage.

Recent petrographic studies (Macdonald and Katsura, 1964) have demonstrated the relationship of rock types to the eruptive history outlined above. The lavas of the shield-building

and most of the caldera-filling stages are tholeiitic basalt (including tholeiite, olivine tholeiite, and oceanite). In the upper part of the caldera-filling sequence, and at a corresponding stratigraphic level outside the caldera, there occurs a change to alkalic lavas (alkalic basalt, olivine basalt, ankaramite, hawaiiite, mugearite, and trachyte), and these rock types persist through the old-age stage. The rocks of the post-erosional stage are characteristically nephelinites and melilite-nephelinites, with associated undersaturated alkalic olivine basalts.

Thus the formation of the calderas, though it may vary somewhat from one volcano to another and may be lacking from some, takes place during the end of the period of shield building, while volcanism is still vigorous, and somewhat before the slowing down of volcanism that accompanies the change of petrographic types from tholeiitic to alkalic.

One important bit of evidence that should be considered in relation to the origin of the Hawaiian calderas is that the caldera floor sometimes moves upward as well as downward. Not only does the floor swell up as a broad flat dome during tumescence of the volcano (Jaggard and Finch, 1929), but it may move en masse in the manner of a huge piston. The great collapse of Kilauea caldera in 1840 produced a central pit 1.5 km wide, 3 km long, and about 150 m deep. About 1845 the floor of the pit started to rise bodily, and by 1850 it had risen about 150 m and was approximately level with the "black ledge" that surrounded it. The taluses that had accumulated on it at the foot of the bounding cliffs had been pushed up until they stood as arcuate ridges of angular rock fragments that projected as much as 45 m above the surrounding caldera floor. Although it is possible that this elevation of the caldera floor could have resulted from shallow intrusion of magma beneath it, as did the elevation of the floor of Halemaumau crater in 1952 (Macdonald, 1955a), it appears more probable that it was caused by inflation of the underlying main magma chamber of the volcano.

#### INTERNAL STRUCTURE OF THE VOLCANOES

In none of the Hawaiian volcanoes has erosion cut deeply enough to expose the congealed

magma body that fed the surface eruptions. Knowledge of the position and nature of the magma chamber is almost wholly implied from seismic evidence and the pattern of swelling and shrinking of the volcano before and after eruptions. Earthquakes originating from a depth of about 60 km below sea level, within the upper part of the earth's mantle, are accompanied by "harmonic" tremor that appears to be the same as the tremor that is known to accompany movement of magma in the volcanic conduits close to the surface. From this it is implied that the magma that feeds the volcano is formed at a depth of about 60 km (Eaton and Murata, 1960). It has long been known that Kilauea volcano gradually tumescs over periods ranging from a few weeks to several years before eruptions (Jaggard and Finch, 1929), presumably because of inflation of an underlying magma reservoir, and detumescs during and after the release of magma by eruption. Recent analyses of the patterns of ground tilting resulting from the tumescence and detumescence, coupled with the depth distribution of the shallow-seated earthquakes that precede eruptions, have led to the conclusion that the top of the magma body lies at a depth of only about 2 km below the summit of Kilauea volcano (Eaton and Murata, 1960). It should be emphasized that this is well above the level of the surrounding ocean floor and consequently well within the mass of the volcanic mountain itself. Room for the magma body must have been obtained either by lateral displacement of its margins or by melting of the rocks that formerly constituted the core of the volcano.

The lateral extent of the magma body is less certain, and indeed it appears doubtful (from inductive reasoning) that it has any sharply defined margin. More likely there is a gradual passage from freely fluid magma to somewhat plastic but essentially solid material, and thence to the truly solid rocks of the volcano's exterior. There can be no question that the magmatic core, or at least material in a very mobile condition, extends outward from beneath the summit of the mountain for many kilometers into the rift zones. Thus, the 1955 eruption of Kilauea from the east rift zone 30 km east of the

caldera was preceded by a marked swelling of the rift zone, with lifting of the ground surface along the crest of the rift-zone arch in the eruption area of more than a foot (Macdonald and Eaton, 1964:105).

There is no real evidence of magma chambers at shallow depths beneath the other Hawaiian volcanoes. Even at Mauna Loa the measurements of tilting are far from sufficient to demonstrate such a chamber. By analogy with Kilauea, however, it may be assumed that such magma chambers probably exist, or did exist when the volcano was active. The collapse of the shield to form the caldera is probably dependent on the existence of this magma body, and the fact that caldera formation does not occur until near the end of the shield-building stage is probably because sufficient remelting of the core of the shield to form the chamber has not taken place until that stage.

During recent years, gravity studies in the Hawaiian Islands have indicated very high values in and near the areas of some of the calderas (Woollard, 1951; Woollard et al., 1964). Strange, Woollard, and Rose (p. 381 in this issue) reports that whereas the average Bouguer gravity anomaly value along the Hawaiian ridge is about +200 mgal, the intensity in the central parts of the Koolau and Waianae calderas, Oahu, is in excess of 310 mgal, and "the maximum Bouguer anomaly values over most of the volcanic centers range between +285 and +325 mgal." He points out, as had Woollard (1951), that to explain the anomalies it is necessary to assume a very high density for the material in the volcanic "pipes." Similarly, Adams and Furumoto (p. 296 in this issue) and Furumoto, Thompson, and Woollard (p. 306 in this issue) find seismic velocities in the Koolau "plug" greater than 7 km/sec, as compared with 4.6 km/sec in surrounding material. Adams estimates the plug to be about 6 km across, with its top about 1.6 km below sea level. Similar high seismic velocities were found by Shor (1960) approaching close to the surface in the northwestern part of the Hawaiian ridge, near the Gardner Pinnacles. To explain the observed pattern of high gravity values combined with high seismic velocities, one is forced to assume

rocks beneath the Oahu calderas with densities approximating 3.2 gm/cc extending to at least the depth of the ocean floor (5.5 km). Very dense caldera-filling tholeiitic basalts may have densities up to a little more than 3, and oceanites have measured densities ranging up to about 3.2; but of Hawaiian rocks only the peridotites found as inclusions in flows have consistently a density greater than 3.2.

The dense high-velocity rock has generally been considered to be part of the earth's mantle injected to high levels in the crust. However, it conceivably could be cumulate material settled from the overlying magma in the conduit and core of the volcano or lagging behind as the more fluid portion of the magma rose around it. Fragments of dunite and wehrlite brought up by lavas of the old-age stage of the volcanoes, such as the 1801 eruption of Hualalai (Macdonald, 1949:76; Richter and Murata, 1961) have textures resembling those of the cumulate rocks of layered intrusives (Wager, Brown, and Wadsworth, 1960) and probably represent fragments of cumulate rock brought up from relatively shallow depths beneath the volcano. The mineral assemblages are not particularly indicative of high-pressure equilibria. On the other hand, the garnet pyroxenite ("eclogite") found as inclusions at Salt Lake Crater on Oahu does represent a high-pressure equilibrium assemblage, and quite probably represents material brought up from the mantle. In chemical composition it is very close to tholeiitic oceanite, though somewhat richer in silica and poorer in alkalis (Macdonald and Katsura, 1964: Table 8, col. 13), and may represent an oceanitic intrusive mass crystallized under high pressure in the upper mantle. Its density (2.71–2.81) and seismic velocity ( $V_p = 5.52$ – $6.06$ ) as determined by Manghnani and Woollard (p. 291 in this issue) are too low to account for the material in the primary volcanic "pipes," which is characterized by high gravity values. Moreover, there is no significant gravity "high" associated with Salt Lake Crater.

Brief mention of the rift zones of Hawaiian shield volcanoes has already been made. The rift zones generally radiate outward from the summit of the shield—that is, from the caldera.

Usually there are three distinct rift zones, with angles of roughly  $120^\circ$  between them, and with one rift zone less well developed than the others. In addition to the lines of spatter cones and cinder cones resulting from eruption, the rift zones are marked by pit craters, many open fissures, and by long narrow grabens. The depth of the grabens is generally unknown, because they have been partly filled with later lava. At depth in the older, dissected volcanoes, the rift zones are marked by thousands of thin dikes. Sections across them yield counts of more than 600 dikes per mile. Although a few instances of strike-slip displacement on rift-zone fissures are known (Macdonald, 1956:278), the configuration of the walls of the dikes generally indicates horizontal opening without any appreciable displacement parallel to the fissure. There can be no question that the rift zones represent a very considerable distension of the visible part of the shield volcano, a distension on the order of 0.75–1 km.

The Hawaiian rift zones have recently been explained by J. G. Moore (at a lecture before the Peninsula Geological Society, Stanford University, January 7, 1965) as the result of landsliding on a gigantic scale. Specifically, he believes that the southern slope of Kilauea is sliding seaward, the fractures on which the movement is taking place steepening to near verticality to form the east rift zone, with graben collapse along the upper edge of the sliding block. The distension in the rift zone he attributes to the southward movement of the block to the south. He supposes that magma makes its way surfaceward along the plane of sliding. Essentially the same suggestion was made for the origin of the southwest rift zone of Kilauea by Stearns and Clark (1930). Without at present entering into any debate on whether or not there is large-scale landsliding going on along the south flank of Kilauea, it appears very unlikely to me that the east rift zone (or any other) can have the origin suggested by Moore. The essentially vertical attitude of the dikes in the rift zones down to the deepest level of exposure on the deeply eroded islands of Oahu and Kauai, a level equal to more than half of the probable depth to the magma chamber at Kilauea, is inconsistent with

such an origin. So also is the fact that the gravity highs that extend laterally as bulges from the highs beneath the calderas usually coincide closely with the surface trace of the rift zones (Kinoshita et al., 1963: Fig. 1; Strange et al., Fig. 1, p. 382 in this issue). Whether the high value of gravity over the rift zones is due to exceptionally dense material at depth or whether it is wholly the result of a large number of dense dikes, if the path of the rising magma were inclined markedly to one side at shallow depth the gravity high should not only lie to one side of the rift zone, but should be only a fraction of the magnitude observed and of much greater width. The close coincidence of the "high" and the surface rift zone, therefore, strongly suggests continuation of the rift zone essentially vertically at depth. Furthermore, before any landslide or landslide-induced rift could exist, there must have been a volcanic mass for the slide to form upon. The east rift zone of Kilauea occupies the top of a gentle constructional arch that extends all the way to the sea floor, more than 100 km east of the summit of the shield. The arch has obviously been built by eruptions from the rift, and the shape of the shield is fundamentally governed by the position of the rift zone. The same is true of the other Hawaiian shields. The shields are generally not round or oval, but lobate, resembling three-pointed stars in ground plan (Wentworth and Macdonald, 1953), as a result of building by eruptions predominantly along the three rift zones. The close dependence in shape of the major shields upon the position of the rift zones indicates that the rifts are earlier-formed and are more fundamental structures than any produced by landsliding.

Displacement of the ground surface during the 1955 eruption on the east rift zone of Kilauea (Macdonald and Eaton, 1964) involved slight elevation of the surface adjacent to the eruptive fissures, sinking of a graben along the rift, and lateral displacement of the ground outside the graben by an amount up to a little more than 1.5 m in a direction essentially normal to the rift. There was no detectable sinking of the surface outside the graben on either side of the rift in relation to the other side.

The predominance of earthquake foci south of the rift zone noted by Moore is probably

related to movement on faults of the Hilina system, which lies along the south slope of Kilauea and converges eastward with the rift zone (Stearns and Macdonald, 1946: Pl. 1), rather than to movement on the rift zone itself. Commonly, groups of earthquakes on the rift zone are quite distinct from those originating farther south, as is clearly shown on the map published by Koyanagi (1964).

The rift zone pattern is closely similar to that resulting from distension of the surface of domes pushed up over intrusions (Cloos, 1955); and the most probable cause of Hawaiian rift zones still appears to be inflation of the volcano by intrusion of magma within it.

#### CAUSES OF CALDERA COLLAPSE

Two principal hypotheses have been advanced to account for the sinking of the summits of the Hawaiian shields to form calderas. Both depend upon the presence of a magma body of at least moderate size at a shallow depth beneath the summit area—a once-hypothetical magma body the actual existence of which now appears to be demonstrated. Williams (1941: 246, 286–292) took the Hawaiian calderas as examples of his calderas of "Kilauean type," which he believed resulted from removal of support caused by drainage of magma from beneath them, caused in turn by rapid effusion on the flanks of the volcano or intrusion as dikes or sills. Stearns and Macdonald (1946: 33) suggested as an alternative explanation that the calderas resulted from weakening of the summit area by large-scale magmatic stoping and cauldron subsidence as in the Scottish ring complexes—calderas classified by Williams (1941: 246) as the "Glen Coe type." The mechanism of their formation was believed to be the upward enlargement of the magma body by stoping and cauldron subsidence until the overlying crust became too thin and weak to support itself, when ring fractures developed and the surficial block sank into the underlying magma because of its greater density. The same mechanism should operate if the enlargement of the underlying magma chamber was largely by stoping of the enclosing rocks instead of by stoping.



Reynolds' (1956) suggestion that the Scottish cauldron subsidences and the calderas that presumably lay above them were formed by the gas-coring mechanism suggested by Escher (1929), with "fluidization," intrusion, and ejection of an ignimbritic solid-gas emulsion, can have no bearing on Hawaiian calderas because of the complete absence in Hawaii of ignimbritic material and the extreme paucity of fragmental explosive material of any sort.

Before considering further these older hypotheses, let us look briefly at a new one. The very high density of the material in pipe-like masses beneath the summit areas of Hawaiian volcanoes has led to the suggestion that the formation of a caldera might be the result of the isostatic sinking of the heavy column, carrying the overlying mountain top down with it. In this connection it is necessary to consider the gravity field found by Kinoshita and others (1963) on the island of Hawaii. Their Figure 1 shows that the gravity high for Mauna Loa (a Bouguer anomaly reaching between 330 and 340 mgal) is offset several kilometers to the southeast of Mokuaweoweo caldera, farther to one side than is the presumed top of the dense material below the surface. There is no sign whatever of sinking of the mountain surface above the center of the gravity high. The high for Kilauea (reaching about 315 mgal) also is excentric to the caldera, the center of the high lying some 2 km or more to the southwest of the center of the caldera. Thus, it appears unlikely that the caldera formation can have resulted simply from isostatic sinking, unless the improbable mechanism of a highly oblique subsidence is invoked. Furthermore, no discernible sinking has disrupted the post-caldera cap on volcanoes such as Mauna Kea, beneath which a markedly high gravity anomaly still exists (Kinoshita et al., 1963). Isostatic sinking in the ordinary sense, therefore, appears improbable as an explanation for the Hawaiian calderas.

The high-density column beneath the volcanoes may have another effect, however. Rising, as it apparently does, some 5 km or more above the base of the volcanic mountain, the base of the mass must have a considerable tendency to spread, and must exert a consid-

erable lateral thrust on the lighter material adjacent to it. This must be particularly true when the mass is still somewhat mushy. Does the tendency for the heavy mass to spread result in spasmodic lateral movements of its lower part into the proximal ends of the rift zones, causing a wedging open of the rift zone and a distension of the volcanic edifice?

The principal reason given by Stearns and Macdonald (1946:29-33) for the rejection of Williams' proposed mechanism for formation of calderas of Kilauean type was the fact that flank eruptions with voluminous drainage of magma are frequent throughout the period of building of the shield, whereas the formation of the caldera takes place only near the end of it. Actually, however, if the formation of the caldera depends on the existence of a magma chamber in the core of the volcano, the absence of such a chamber in the earlier stages would account for the absence of a caldera. Considerable time must be necessary for enlargement of the chamber to the point where its roof is too broad and thin to support itself.

A more conclusive argument can be made against the application of the Glen Coe mechanism to Hawaiian calderas: namely, the fact that the sinking caldera block must displace an equal volume of magma. Where does this magma go? Does it rise into the ring fractures around the sinking block, as in the classical interpretation of the cauldron subsidence of Glen Coe (Clough, Maufe, and Bailey, 1909: Fig. 14)? There is no evidence to suggest it. Dikes are nearly absent along the caldera boundaries at levels exposed by erosion. Eruptive vents on the caldera-boundary fractures are very rare, and the few that are found appear to have no fundamental relationship to the fracture. Thus, although the main cone of the 1949 eruption of Mauna Loa lies on the caldera boundary, the eruptive fissure was not the caldera-boundary fissure, but one that extended across the center of the sunken caldera block, up over the caldera wall, and several kilometers down the flank of the mountain. But if the displaced magma does not rise around the sinking block, where does it go? Out into the rift zones? This brings us right back to Williams' Kilauean mechanism!



The failure of magma to rise along the caldera-boundary fractures itself calls for an explanation. The erupting basaltic magma has a specific gravity of about 2.7, and it appears likely that the magma even at the depth of the magma chamber has a density of only about 2.73 (Macdonald, 1963:1076). Compared with this, the gross density of the caldera-filling rocks is at least 2.8, and probably is between 2.9 and 3.0. If a mass of this density is underlain by a magma body of equal or greater horizontal dimensions and lower density, why does not the caldera block sink completely into the magma? The answer probably lies in the wedge form of the sinking block, bounded by fractures that dip inward instead of outward. Reynolds (1956) has pointed out that a downward convergence of the boundary fractures is implied by the up-bending of the edges of the lava beds filling many cauldron subsidences, including that of Glen Coe. The margins of the older, eroded Hawaiian calderas are seldom well enough exposed to reveal whether or not the edges of the beds are bent upward. However, Stearns (1940: Fig. 7) has described a basining of the lavas in the Koolau caldera, Oahu, and at least in one sector the beds filling the Kauai caldera are dragged slightly upward against the caldera boundary (Macdonald, Davis, and Cox, 1960:36). There is a definite implication that the boundary faults converge downward. Since sinking of a wedge-shaped block would tend to keep the boundary fractures tightly closed, this would also help to explain the failure of magma to rise to the surface along them and the lack of eruptive vents on the caldera boundary.

Why do the fractures converge downward, instead of diverging in the ring-dike manner deduced mathematically by Anderson (1936)? Perhaps the answer lies in the fact that the fractures were first established as a result of upthrust of magma beneath a relatively small portion of the mountain top, resulting in upward-divergent fractures of cone-sheet type, and that once established these fractures served as the surfaces on which the caldera block later sank. The tumescence frequently observed at Kilauea shows that magmatic pressure is great enough to push up the top of the mountain,

and the piston-like rise of the caldera floor in the 1850's shows that at times the elevation takes place by displacement of a fault-bounded block rather than by quasi-plastic arching. Where upward pressure continues long enough cone sheets may form, like the numerous concentric inward-dipping dikes that surround the caldera of the Ofu-Olosega volcano in Samoa (McCoy, 1965); and concentric lines of spatter and cinder cones may form by surficial eruption on these fractures, as on some of the volcanoes of the Galapagos Islands (H. Williams, personal communication, 1964). In Hawaii, however, only a few dikes with the attitudes of cone sheets have been found, on Oahu and Kauai. Even fewer examples are known of eruption on concentric fractures, but one such line of cones lies just southwest of Kilauea caldera. For some reason, in Hawaii magmatic pressure has usually resulted in distension of the volcanic structure by upward bending of the summit followed by splitting open of the rift zones instead of lifting of the apex of the volcano on inward-dipping conical fractures.

A factor that must be explained before we can accept Williams' Kilauean mechanism is the very considerable discrepancy that exists between the volumes of some of the subsidences in the caldera during historic times and those of the simultaneously-erupted lava flows. The volumes of historic subsidences are listed in Table 1, the figures being taken from papers by Finch (1940, 1941) except the one for 1955, which is from Macdonald and Eaton (1964). The volumes for 1924 and 1955 include both marked collapses at Halemaumau and a general sinking of the whole mountaintop over a radius of 15 km or more, but this was undetectable without instrumental measurements in the earlier episodes of collapse. In these the figure given is only for the conspicuous sinking that took place in the caldera. Undoubtedly, however, a wider-spread general subsidence, like those in 1924 and 1955, also took place during each of the earlier episodes of collapse, and the volumes of those were accordingly greater than shown. The volumes of the lava flows are taken from Stearns and Macdonald (1946), again except for that of 1955. They include estimates of the volume of subaerial flows that

entered the ocean; but the volumes, and even the existence, of any eruptions that may have taken place below sea level are wholly unknown.

A mere glance at Table 1 shows that there are large discrepancies between the volumes of several of the collapses and those of the accompanying lava flows. The smaller of the discrepancies, such as those for 1840 and 1955, can reasonably be attributed to intrusion of magma as dikes in the rift zones. The volume of extrusion in 1868 can only be guessed at, because we do not know the depth of the fill in Kilauea Iki crater. However, the eruption on the southwest rift zone had a volume of less than 200,000 m<sup>3</sup>, and that in Kilauea Iki cannot be reasonably assumed to have been much more than 5,000,000 m<sup>3</sup> and may well have been a good deal less than that, so that we are left with a discrepancy of something more than 180,000,000 m<sup>3</sup>. This also could be accounted for by the intrusion of an unusually large dike, averaging about 2 m thick and 2 km high above the top of the magma chamber, and extending 45 km across the top of the volcano. (Both rift zones opened during the eruption.) The volume of lava erupted above sea level in 1832 also is not accurately known, but it was very small. Furthermore, the only known vents were above the level of the caldera floor, so that eruption from them can hardly be considered a simple draining of magma from beneath the caldera block, allowing the latter to sink. On the other hand, the sinking of the block may have helped squeeze some magma to the surface. In 1924 there was no eruption of lava whatever above sea level. The discrepancies between the subsidences of 1823, 1832, and 1924 and the volume of known contemporaneous lava flows above sea level are, respectively, more than 525 million, approximately 580 million, and 200 million m<sup>3</sup>. During the 1924 subsidence the east rift zone opened for a distance of more than 45 km, to and beyond the east cape of the island, and Jaggar (1934) believed that a submarine eruption occurred. It is certainly a distinct possibility, and the same could have happened during any of the other episodes of subsidence. An eruption in deep water would quite likely have escaped detection. The volume discrepancies can reasonably be attrib-

uted to rift-zone intrusion and/or submarine eruption.

Thus, the facts that must be taken into consideration in a theory explaining caldera formation appear to be: Caldera collapse takes place generally, if not always, following a period of tumescence of the volcano, accompanying or directly following an opening of one or both of the main rift zones, commonly accompanied by subaerial flank eruption and/or possible submarine eruption; and the sinking takes place on fractures that converge downward, which in turn means that sufficient outward movement of the circumferential mass must take place to make room for the increasing diameter of the sinking wedge at any given level. The distension of the summit region is very probably a part of, and is caused by the same mechanism as, the simultaneous distension of the rift-zone regions. Although eruptions are nearly always accompanied by a general sinking of the mountain-top, caldera collapse may not take place. Eruption may be confined to the caldera or the immediate summit region without any apparent opening of the rift zones, or opening of the rifts only close to the caldera.

The following possible interpretation of the above facts, together with the other facts as to the general structure of the volcano presented earlier, is suggested. Magma very rich in olivine crystals rises from the mantle into the volcano, adding to the bulk of the ultra-dense core; and part of the liquid portion of the magma rises on upward, leaving behind most of the load of solid crystals, to form a pool of fluid tholeiitic basalt in a high-level magma reservoir at the top of the ultra-dense core or, in some volcanoes, somewhat to one side of the top of the core, beneath the summit of the shield and extending outward beneath the near-summit portions of the rift zones. The volcano swells in response to the addition of magma. Local cupolas on the magma body may rise high enough to perforate the roof, allowing long-continued open-vent activity such as the lava lake that existed in Halemaumau crater most of the time through the 19th and early part of the 20th centuries, or the eruption in Mokuaweweo during most of 1873 and 1874. Occasional withdrawals of

magma from the cupolas may allow the collapse of pit craters in and near the caldera and along the rift zones. Eventually the top of the mountain splits open and some of the fluid tholeiitic magma rises to the surface, allowing the volcano to detumescence. The force that drives the magma to the surface is primarily the hydrostatic pressure on the magma body resulting from the weight of the overlying rocks, but as the magma gets very close to the surface there is added to this the expansive force of the gas that is separating from solution. Eruptions of this type are confined to the summit region.

As the mass of ultra-dense material in the core of the volcano grows, from time to time its weight becomes sufficient to cause a slight pushing apart of its confining walls in the lower part of the volcanic structure. This results in a splitting open of the volcano as a whole, including one or both of the rift zones and the summit region. Magma drains outward into the rift zones, and commonly flank eruption results. The volcano detumescence, and if distension of the summit region has been sufficient to allow sinking of the wedge-shaped caldera block true caldera collapse ensues. At other times, without any appreciable downfaulting of the caldera block, the detumescence may be simply a gentle over-all sinking detectable only by instrumental methods (as it commonly is in the case of summit eruptions); or it may be accompanied by marked collapse only at points where the underlying magma body approaches or reaches the surface, such as the collapse of Halemaumau crater during the subsidence of 1924 or the basining of the caldera floor in 1868 and 1894. Sinking of the caldera block depends on distension of the summit more than on draining away of the underlying magma, since the heavy rock of the caldera fill can sink indefinitely into the less dense magma. However, sinking of the caldera is generally accompanied by lateral movement of the underlying magma into the rift zones because the same lateral displacement that stretches the summit region enough to allow sinking of the caldera block also opens the rift zones, and room for the sinking is largely provided by drainage of magma into the rift zones. Some magma is squeezed out in the summit region by sinking

of the overlying rocks, but the denseness of the caldera-filling rocks and the wedge shape of the sinking block keeps the underlying conical subsidence fractures tightly closed and largely prevents the rise of magma through them. Discrepancies between the volume of summit sinking, including caldera collapse, and the volume of lava extruded in subaerial eruptions (both flank and summit) are accounted for partly by intrusion into the rift zones, probably partly by submarine eruption, at times partly by squeezing of magma upward into fissures in overlying rocks, and partly by space provided by the slight sinking of the top of the ultra-dense core as a result of spreading of its lower portion.

The eruption is brought to an end by drainage of the easily-eruptible magma down to the level of the opening of the fissures, but the eruption may be prolonged by rise of additional magma from deep levels, as appears probably to have been the case during the 1959 eruption in Kilauea Iki (Richter and Eaton, 1960). Afterward the volcanic structure is sealed by partial or complete congealing of magma in the fissures, and the whole cycle repeats itself as more ultra-dense magma rises from the mantle and more tholeiitic magma accumulates in the shallow magma reservoir.

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# Seismic Reflection Studies of Sediment Thickness Around the Hawaiian Ridge<sup>1</sup>

LOREN W. KROENKE

DURING THE SPRING AND SUMMER of 1964, seismic profile surveys of sediment thickness were made on board the Research Vessel "Neptune I" around the Hawaiian Ridge. The seismic-reflection profiling techniques were based on a shallow explosive sound source of 1/2-lb blocks of TNT. The recording equipment was a modified facsimile drum recorder similar to that described by Ewing and Tiery (1961). The detector was an array formed with eight hydrophones enclosed in an oil-filled polyvinyl-chloride tube.

<sup>1</sup>Hawaii Institute of Geophysics Contribution No. 93.

The positions of seven tracks along which data were obtained are shown in Figure 1. The data obtained are presented in Figures 2, 3, and 4 in the form of profiles, with the vertical scales showing two-way travel time in seconds and the horizontal scales indicating position time for the vessel in hours. No corrections have been made for variations in the velocity of sound in sea water.

Because sedimentary velocities are not well determined for the area around the Hawaiian Swell, an average velocity of 2 km/sec has been assumed, based on available data from refrac-

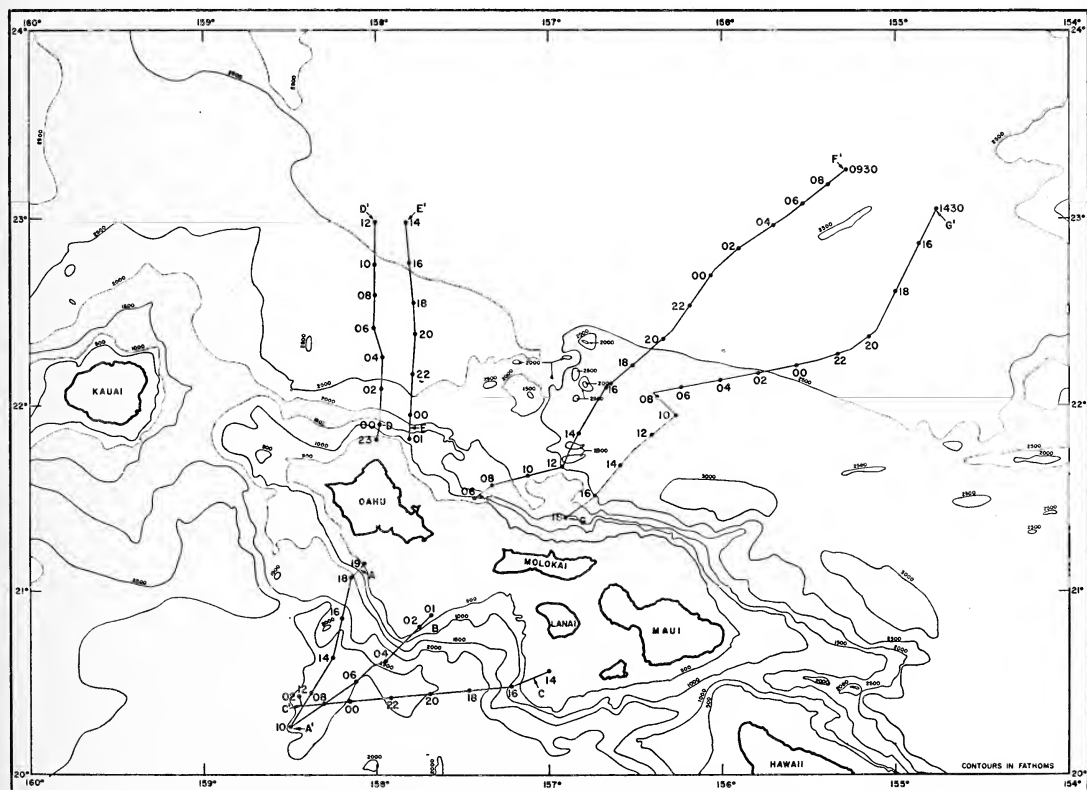


FIG. 1. Chart showing tracks of R/V "Neptune I," with 2-hourly positions, during seismic reflection profiling cruises.

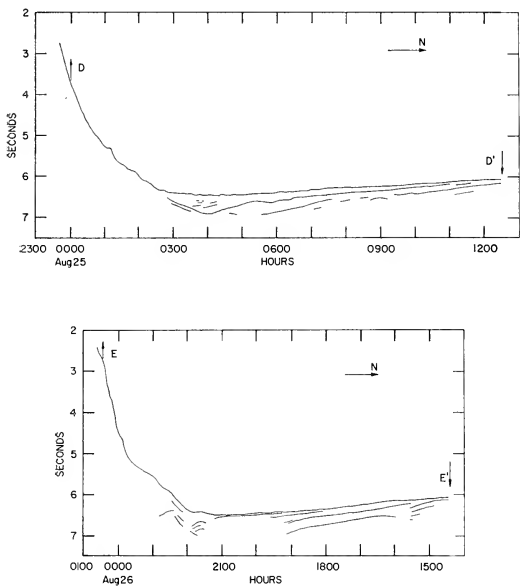


FIG. 2. Seismic reflection profiles north of Oahu.

tion seismic measurements made mostly north of the Hawaiian Ridge.

Little to no thickness of sediments is indicated in the shallow water over Penguin Banks southwest of Molokai. The area appears to be characterized by a high degree of bottom reflectivity, and high reverberation level. This may have masked any thin veneer of sediment that might be present. On the island shelf north of Molokai and Maui and within the Molokai Channel, sporadic sediment accumulation occurs and varies from 100–160 m in thickness. This appears to be concentrated in pockets and channels along the shelf. For the most part, the bottom again exhibits a relatively high degree of reflectivity.

Reefs are thought to be observed at the south edge of Penguin Banks southwest of Molokai and at the edge of the shelf north of Maui. Southwest of Molokai the reef appears to be 230 m thick, with the top lying 500 m below sea level. North of Maui the reef appears

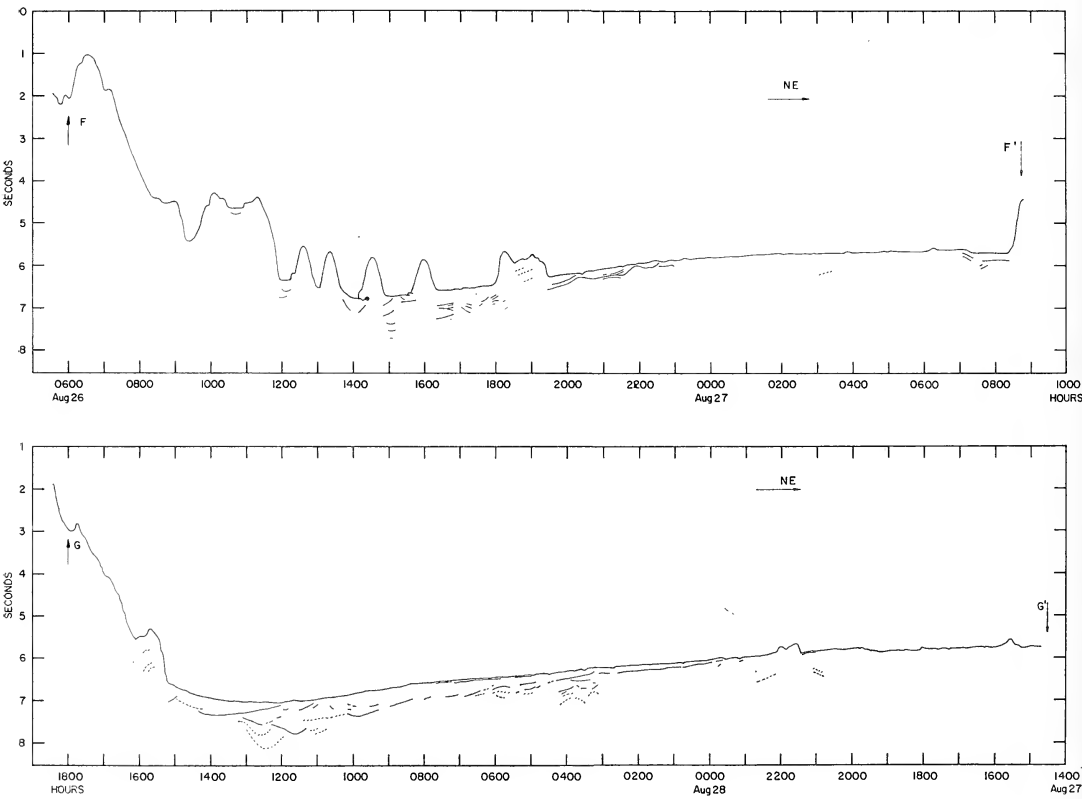


FIG. 3. Seismic reflection profiles northeast of Molokai.

to be 90 m thick, with the top 440 m below sea level. No bottom samples were obtained to verify the profile results. However, Menard et al. (1962) have reported Miocene (?) fossils dredged southwest of Honolulu at a depth of 500 to 520 m. If the seismically defined reefs are real and could all be shown to be of equivalent age, differential subsidence along the length of the Hawaiian Ridge, of at least 440 m north of Maui to 500 m south of Oahu, is indicated since the advent of reef formation. In their paper, Menard et al. suggest that dredge-hauls south of Oahu were from a Miocene reef *in situ*. If this is true, then approximately 0.5 km of subsidence has occurred since Miocene time, which leaves at least 1.5–2.5 km of subsidence to be explained as having occurred before reef formation (to be in accord with the total subsidence of 2–3 km suggested by seismic-refraction measurements).

The fact that subsidence of more than 0.5 km has taken place is also shown by the reflection measurements in the flanking trench-areas to the north and south of the Hawaiian Ridge. In both areas a considerable thickness of sediments is indicated. Two parallel profiles made due north of Oahu (Fig. 2) show depths to the lowest sub-bottom reflecting layer to be in excess of 600 m within the deeps, thinning to less than 100 m up the south flank of the Hawaiian Arch. A similar situation is observed on two profiles northeast of Molokai (Fig. 3). Here the deepest sub-bottom reflecting layer appears to be in excess of 1 km, thinning to zero as the crest of the Arch is reached.

These results are in agreement with the conditions postulated by Shor and Pollard (1964) from seismic refraction measurements.

South of the Hawaiian Ridge the sediment thickness varies from 100–200 m in thickness. Probably this indicates a less active environment of deposition, as the over-all picture is similar to that north of the Ridge. Both north and south of the Hawaiian Ridge the sediment thickness increases as the base of the Ridge is approached. Although it is more obvious in the northern profiles, the sub-bottom topography continues to dip toward the Ridge on both sides until the base of the slope is encountered. This is suggestive of faulting at the base of the

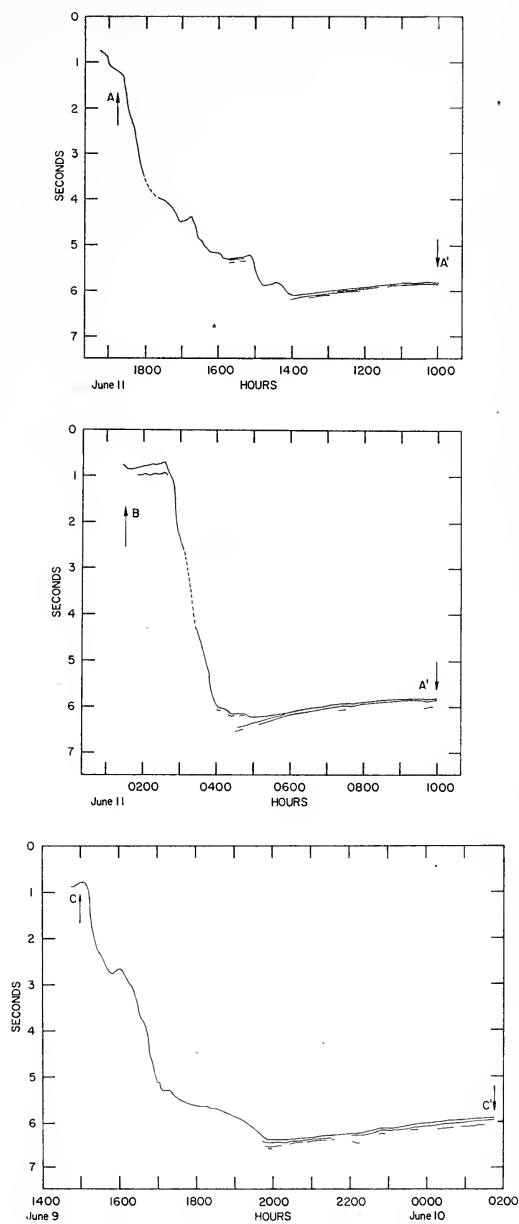


FIG. 4. Seismic reflection profiles south of Oahu (A, B) and Molokai (C).

slope. An alternate explanation would be a simple migration of the axis of a depositional basin inward toward the Hawaiian Ridge as the Ridge sank. Although slumping or volcanic flows appear to mask most of the base of the Ridge, the sub-bottom sedimentary structure strongly suggests progressive downwarped-



ing of the crust on both sides of the Hawaiian Rise as the island platform of the Ridge was built up.

#### ACKNOWLEDGMENTS

The work reported here was carried out under Contract ONR 3748(05) with the Office of Naval Research.

This paper represents a cooperative effort on the part of Hawaii Institute of Geophysics personnel. In particular, thanks are due Mr. William Strange and Mr. L. Machesky for their assistance on shipboard and with interpretation of the data. The author is also grateful to Captain Roy Coe and the crew of the R/V "Neptune" for their cooperation and help

during the explosives operation. Finally, the valuable support and encouragement furnished by Dr. G. P. Woollard can never be fully acknowledged.

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# A Gravity Survey of the Island of Hawaii<sup>1</sup>

W. T. KINOSHITA

A BOUGUER ANOMALY CONTOUR MAP, based on a gravity survey made on the island of Hawaii during parts of 1961 and 1962 (Kinoshita et al., 1963), is presented as Figure 1. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 1). Measurements along the main roads and trails provided generally good coverage at elevations below 6000 ft, but at higher elevations large areas are inaccessible, and the gravity map is necessarily generalized.

About two-thirds of the stations were located at bench marks or spot elevations published on standard 1:24,000 scale U. S. Geological Survey topographic quadrangle maps. The rest were located at similar points on 1:62,500 scale maps. All of the gravity measurements were made with a LaCoste Romberg gravimeter relative to a base station at the Hawaiian Volcano Observatory, which has an observed gravity value of 978,664.42 mgal. Topographic and Bouguer corrections were made in the same manner as those on Maui (Kinoshita and Okamura, pp. 000 in this issue) with the exception that topographic corrections were made at about 50% of the stations instead of at 15% as on Maui. In the table the complete Bouguer anomaly is given to 0.1 mgal at those stations where the topographic correction was calculated, and to the even mgal where they were estimated.

The gravimeter was read at the base station several times during the course of approximately 30 days of field work and the maximum variation in the readings was 0.7 mgal. Corrections for instrumental drift and tidal effects

were neglected in the calculations; their combined effects could be as large as 1 mgal. Although the maximum variation in base readings was as much as 0.7 mgal, about 90% of the readings were within 0.2 mgal. Thus, any one observed gravity value could be in error by as much as 1 mgal, but is probably correct to within 0.5 mgal. Most of the published elevations are accurate to within 5 ft of their true elevations, but for the parts of the island where only the smaller scale topographic maps were available, the elevations could be in error by 15 ft. In terms of a combined free-air Bouguer correction, these elevation uncertainties would correspond to errors of about 0.3 mgal and 1 mgal, respectively. Topographic corrections are probably correct to within 10%. Hence the largest topographic corrections, such as the 50- to 60-mgal values obtained at the summits of Mauna Loa and Mauna Kea, can introduce errors up to 6 mgal. However, most of the stations had topographic corrections of less than 20 mgal, so the complete Bouguer anomaly value at any one station is probably accurate to at least 3 mgal.

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<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.

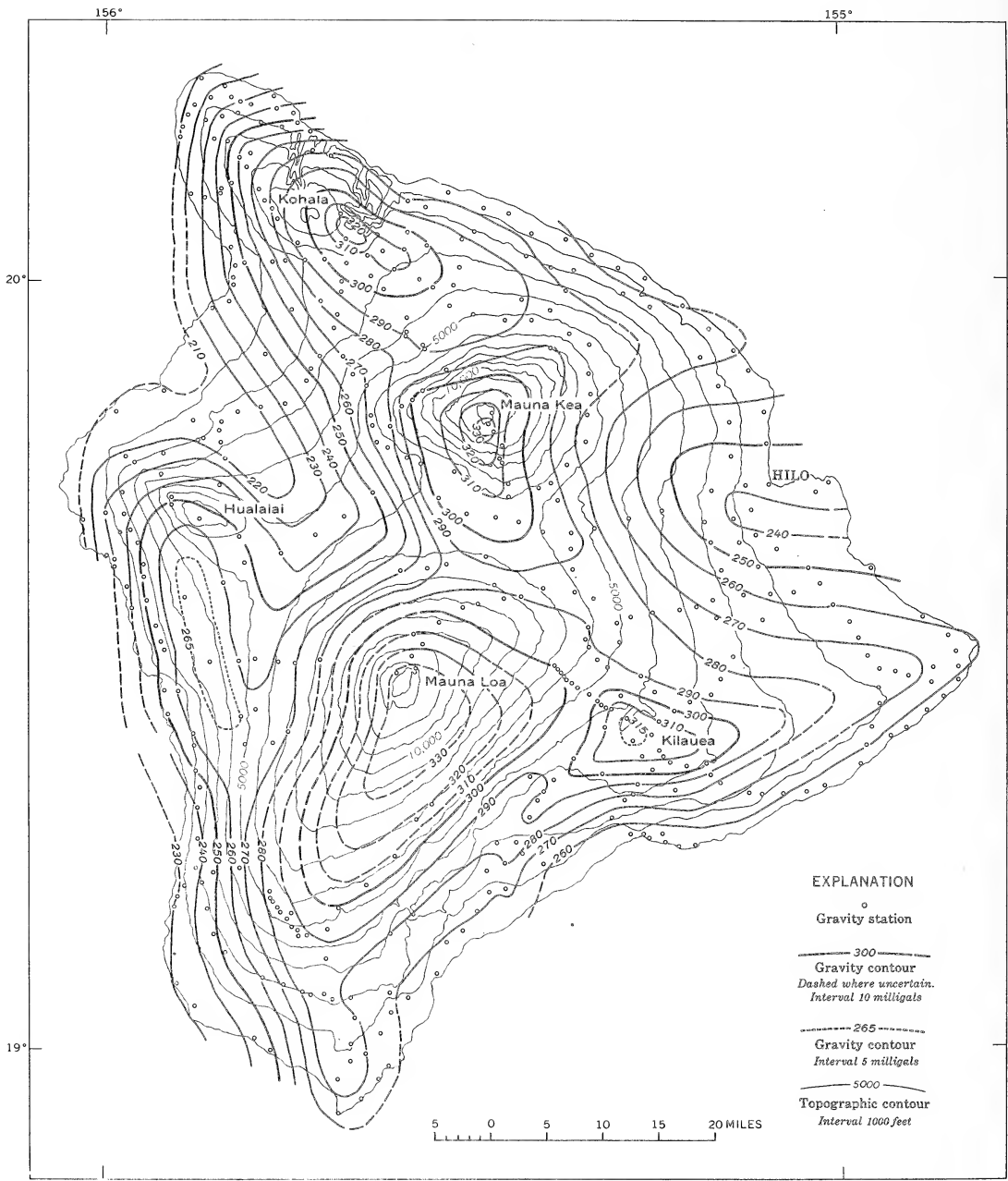


FIG. 1. Bouguer gravity-anomaly map of the island of Hawaii.

# A Gravity Survey of the Island of Maui, Hawaii<sup>1</sup>

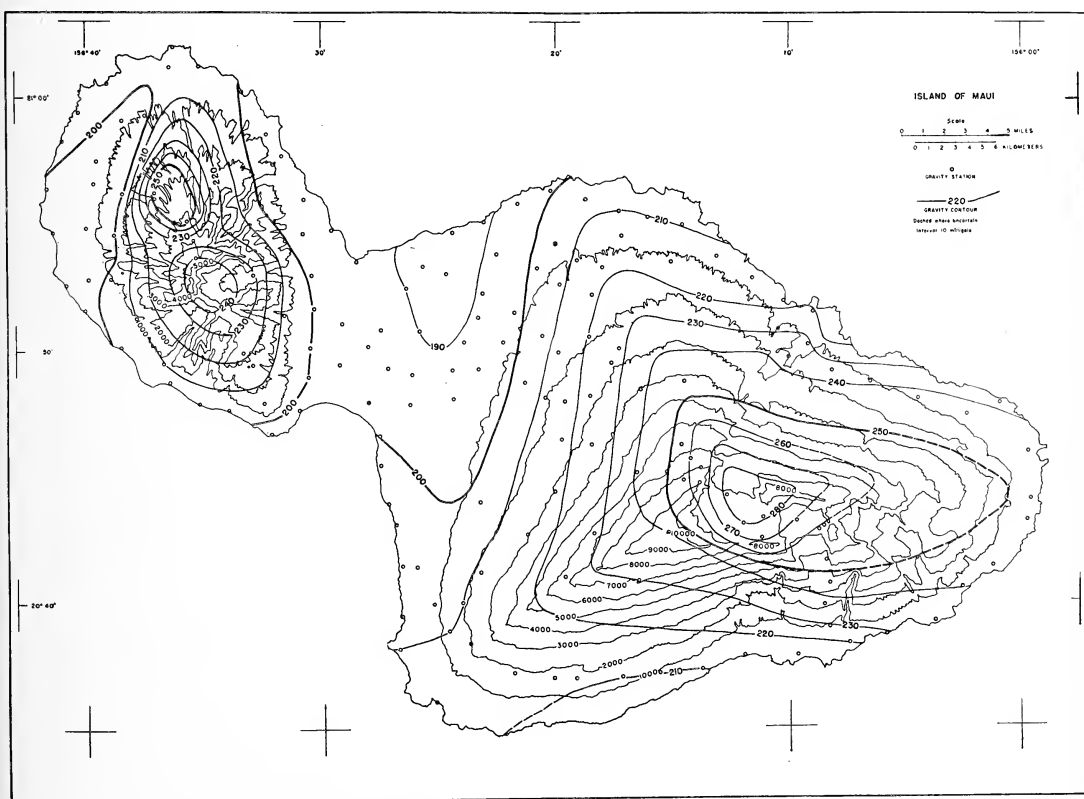
W. T. KINOSHITA and R. T. OKAMURA

A BOUGUER ANOMALY CONTOUR MAP, based on gravity measurements made on the island of Maui during February 1962, is presented as Figure 1. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 2). Gravity measurements were made, using a LaCoste Romberg gravimeter, along most of the main roads and along a few foot trails at the summit of West Maui and inside Haleakala Caldera on East Maui. The relative inaccessibility of parts of the volcanoes, especially at the higher elevations, made the gravity station coverage sparse in those areas. Thus the depicted gravity contour pattern is strongly influenced by

the measurements made at the lower elevations.

Most of the stations were located at bench marks or spot elevations published on standard 1:24,000 scale U. S. Geological Survey topographic quadrangle maps. A few stations (U153, U155, U157, U159, U160, U161, U204, U207, U208, U209) were established at identifiable points and plotted on topographic maps. The elevations of these stations were determined by altimetry. All of the gravity measurements were made relative to a base station with an observed gravity value of 978,889.27 mgal which was established at the Kahului airport in 1961 by R. R. MacDonald (personal communication). The gravimeter was read at the base station at the beginning and end of each day,

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.



and the readings varied by less than 0.15 mgal during the six days of the field work. Corrections for instrumental drift and tidal effect, therefore, were neglected in the calculations, as their combined effects amount to only a few tenths of a mgal. The data were corrected for elevation above sea level and effects of above-sea-level terrain within about 100 miles of each station. An assumed average rock density of 2.3 g/cc was used in the Bouguer and topographic corrections. Topographic corrections were made at about 15% of the stations; corrections at other stations were estimated on the basis of the calculated corrections.

Observed gravity values are believed to be accurate to at least 0.5 mgal. The elevations of bench marks and spot elevations are known within  $\pm 5$  ft of their true elevations, and the altimeter-determined elevations are believed to be accurate within  $\pm 25$  ft. In terms of a com-

bined free-air Bouguer correction, these elevation uncertainties would correspond to errors of 0.3 mgal and 1.6 mgal, respectively. Topographic corrections are probably correct to within 10%. Hence, the largest topographic corrections, such as the 40- to 50-mgal values obtained at the summits of West Maui and Haleakala volcano, can introduce errors up to 5 mgal. However, most of the stations had topographic corrections of less than 20 mgal, so probably the complete Bouguer anomaly value, at most stations, is accurate to at least 3 mgal.

#### REFERENCE

- HAWAII INSTITUTE OF GEOPHYSICS. 1965. Data from gravity surveys over the Hawaiian Archipelago and other Pacific islands. Hawaii Inst. Geoph. Rept. 65-4, March 1965. 10 tables.

# A Reconnaissance Gravity Survey of the Island of Molokai, Hawaii<sup>1</sup>

JAMES G. MOORE<sup>2</sup> and HAROLD L. KRIVOV<sup>3</sup>

DURING DECEMBER, January, and February, 1962–1963, 72 gravity measurements were made with a La Coste and Romberg meter (G-8) on the island of Molokai. Stations were located and elevations determined on 1:24,000 scale modern topographic maps. A gravity station (No. 23) at the Molokai airport (Fig. 1), first established by R. R. MacDonald, was used as the primary base during the course of the survey. Because of limited time and the inaccessible nature of much of the island, especially the eastern part, the present survey is of a reconnaissance nature only. However, enough data are available to outline roughly the general gravity field of West Molokai Volcano and to permit speculation on that of East Molokai Volcano.

The help of the following residents of Molokai is gratefully acknowledged: Edward Burlem, Superintendent of Kalaupapa Settlement; James Linebaugh and Sakuichi Nakamura, Soil Conservation Engineers; and Henry Meyer, Operations Manager of Molokai Ranch.

## GENERAL GEOLOGY

Molokai, situated southeast of Oahu, is the fifth largest of the Hawaiian Islands and consists of two shield volcanoes arranged along an east-trending line (Fig. 2). West Molokai Volcano is built mainly of thin basalt flows which dip gently from the high point of the volcano. It is flatter than most Hawaiian volcanoes and apparently the summit was never indented by a caldera (Stearns and Macdonald, 1947:15). K-Ar ages (McDougall, 1964) indicate that the last eruptions of West Molokai Volcano occurred about 1.8 million years ago.

Two rift zones marked by broad ridges radiate from the summit of the western volcano,

one to the northwest and the other to the southwest. Numerous dikes have been mapped (Stearns and Macdonald, 1947) along the coast from 1 to 5 miles east of the northwest cape of the island along the trend of the northwest rift zone. No dikes have been mapped on the southwest rift, but a few dikes are exposed along the south coast and may define a possible southeast rift zone of the volcano.

On the northeast side of West Molokai Volcano are many faults which are downthrown chiefly toward the northeast (Fig. 2). They indicate collapse of the northeast slope and summit area of the volcano, apparently before East Molokai Volcano had attained its present size.

East Molokai Volcano is composed of two volcanic series, a lower unit of olivine basalts, and a relatively thin upper unit dominantly of mugearite and trachyte. The latest lavas are distinctly younger than those of West Molokai Volcano and overlap its east flank. K-Ar ages (McDougall, 1964) of the exposed rocks of East Molokai Volcano are 1.3–1.5 million years. These lavas were erupted from a central caldera complex, and from the west and east rift zones which intersect at the summit. These rift zones are marked by dikes and cinder cones (Stearns and Macdonald, 1947); Macdonald (1956:16) has suggested that another rift zone extends south from the summit.

On the north shore of East Molokai Volcano several faults dip south and are downthrown on their south side (Fig. 2). Especially thick lava flows are present here, where lava flowing north from the summit of the volcano ponded on the downthrown blocks.

The latest volcanic activity on the island of Molokai occurred north of the great sea cliff on the north side of East Molokai Volcano. A small vent 1 mile east of Kalaupapa extruded olivine basalt lava which built the low Kalaupapa peninsula nearly 3 miles north of the base of the sea cliff.

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.

<sup>2</sup> U. S. Geological Survey, Menlo Park, California.

<sup>3</sup> U. S. Geological Survey, Denver, Colorado.

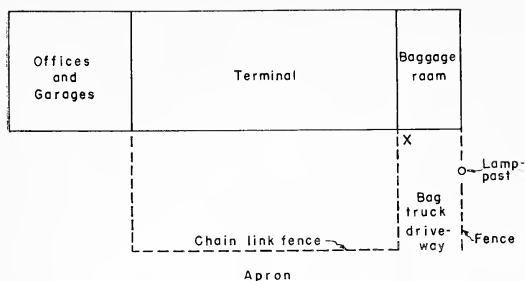


FIG. 1. Plan of Molokai airport. X, site of gravity station No. 23.

### GRAVITY

A Bouguer gravity map (Fig. 3) was prepared for the island from gravity measurements from 72 stations. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 3). As with gravity surveys of the island of Hawaii (Kinoshita et al., 1963), a density of 2.3 g/cc was used for the Bouguer corrections. No systematic tidal, drift, or terrain corrections have been made.

Like other Hawaiian volcanoes, West Molokai Volcano shows a well-marked gravity high near the center. This anomaly presumably represents the higher percentage of denser intrusive rocks and perhaps ponded lavas associated with the magma reservoir and central conduit of the volcano. This anomaly, however, lies considerably east of the high part of the volcano and,

in fact, is largely within the area of extensive faulting on the northeast flank of the volcano. Much of this central positive gravity anomaly lies in the area covered by the younger lavas of East Molokai Volcano. The relationship of the fault system on the northeast flank of West Molokai Volcano to the gravity-defined volcanic center suggests that these faults, probably caused by gravity sliding to the north, encroached on the volcanic center in much the same way as the Hilina fault system is encroaching on the south flank of Kilauea Volcano (Moore and Krivoy, 1964:2043).

Gravity noses trending northwest and southwest from this central gravity high (Fig. 3) presumably define the major rift zones of West Molokai Volcano. A gravity nose extending to the east may represent an east rift zone of the west volcano, but in this region of overlap the possibility that this structure belongs to East Molokai Volcano cannot be eliminated. Control of gravity measurements on the south coast of West Molokai is insufficient to test the presence of a southeast rift zone.

The gravity measurements on East Molokai Volcano are few and are restricted chiefly to the south and east coastal region and to the Kalau-papa peninsula to the north. No gravity measurements were made near the mapped caldera complex and the character of the central gravity configuration is not known. Terrain corrections have been computed for four stations on East

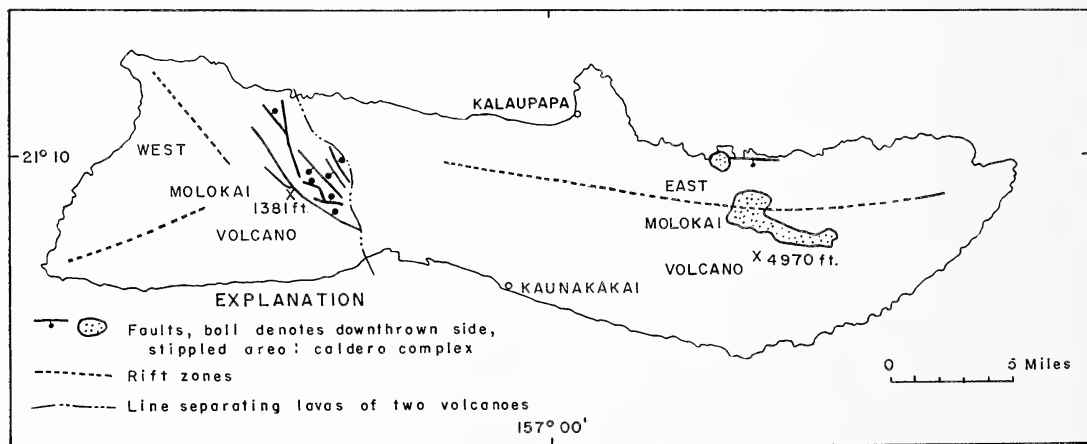


FIG. 2. Geologic sketch map of the island of Molokai. After Stearns and Macdonald (1947) and Stearns (1946).

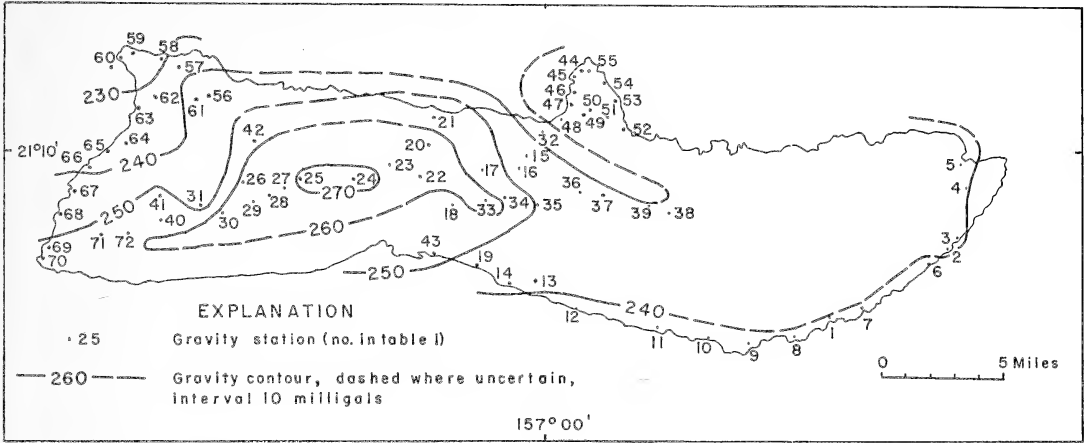


FIG. 3. Bouguer gravity anomaly map of the island of Molokai, Hawaii.

Molokai. These stations with terrain corrections in milligals are: No. 3, +1.6; No. 38, +16.5; No. 49, +4.6; and No. 55, +0.8. The terrain effects are particularly large in the central, rugged part of East Molokai, and here uncorrected values must be used with caution.

The gravity data on the south and east flanks of East Molokai Volcano are insufficient to define any rift zones. Although the coverage is incomplete, the data suggest that the rift zone on the west side of the volcanic center extends west-northwest from the summit of East Molokai Volcano through the Kalaupapa peninsula. The vent which extruded the lava flows that built the Kalaupapa peninsula was presumably fed by magma moving from the volcanic center through this rift zone.

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# A Preliminary Gravity Survey of the Island of Lanai, Hawaii<sup>1</sup>

HAROLD L. KRIVOV and MICHAEL P. LANE<sup>2</sup>

THE GRAVITY VALUE of the base station at Kahului Airport, Maui, was measured at 978.88927 gal by R. R. MacDonald and W. T. Kinoshita in 1961 and 1962 (written communication). Gravity differences measured between Maui and Lanai during this survey confirm the base value of 978.84757 gal established by R. R. MacDonald at Lanai Airport in 1961. LaCoste and Romberg gravity meter G-8 was used to establish both of these base stations. Figure 1 shows the location of both gravity bases used on Lanai; the Lanai Inn base was used for control before and after each day's survey. Table 1 lists the date, time, and reading in milligals at the base station (Lanai Inn) from which all of the loops on Lanai were originated. These data are introduced to demonstrate the drift-free behavior of the meter. Gravity meter readings were not corrected for instrumental drift because the drift would involve errors of the order of tenths of a mgal, whereas uncertainties in elevation and in station location could introduce errors of the order of 1 mgal. The reconnaissance nature of the survey, as well as the size of the gravity anomalies anticipated, obviated the necessity for the drift and tidal corrections which would have been needed for a more detailed gravity study where elevation, location, and bulk density were better known.

The table of principal facts for the gravity survey on Lanai is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 4). A few U. S. Geological Survey and U. S. Coast and Geodetic Survey benchmarks and triangulation stations were located and occupied. Other stations were at rain gauge sites maintained and surveyed by the Lanai Plantation, Dole Corporation. The

Plantation field maps were the most recent charts available for this gravity survey, and the rain gauge sites shown on them were convenient in number and distribution for use as gravity stations. The present engineering staff of Dole Corporation is not certain how the rain gauges were located or how their elevations were determined. It seems probable that the majority of the rain gauges were located by horizontal triangulation and that their elevations were then read from existing (1921, 1940) U. S. Geological Survey topographic maps of the island. Uncertainties lead to the possibility that any station may be in error by as much as 10 ft of elevation. Adjacent stations could have a relative elevation error as large as 20 ft. An error of 20 ft in elevation would be the equivalent of about 1.3 mgal.

At the latitude of Lanai a change of 1' in latitude is roughly equal to 1 mgal in theoretical gravity. Gravity errors due to mislocation, therefore, would probably be less than a few tenths of a mgal. Gravity errors resulting from errors in both elevation and location could be as large as 2 mgal.

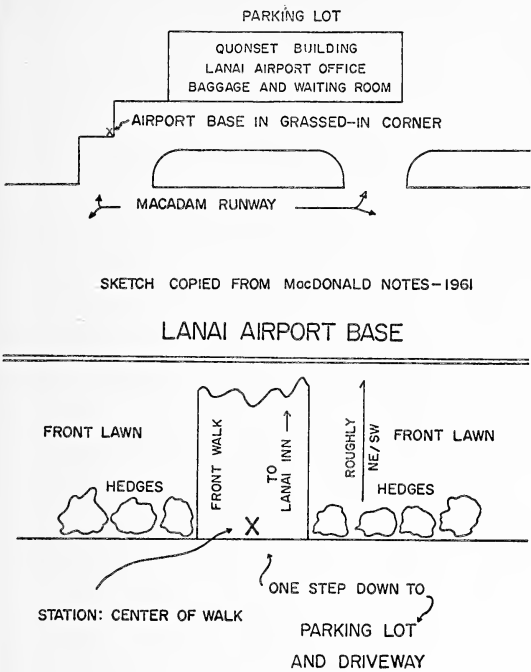
Woollard (1951) used a density of 2.3 g/cc to reduce gravity data for Oahu to a sea level datum. He based that choice on gravity profiling computations using Vening Meinesz' submarine data. Gravity data on the island of Hawaii were reduced on the same basis of 2.3 g/cc (Krivov and Eaton, 1961). Recent density determinations appear to confirm that choice. On Lanai the choice of bulk density to sea level is complicated by a rather thick weathering zone which seems to cover the island with varying depths of low density soil, talus, and detrital fill.

## THE EFFECT OF VARIOUS DENSITIES ON THE BOUGUER GRAVITY MAP

Thus far, other Hawaiian volcanic units studied with gravity methods have been mapped on

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.

<sup>2</sup> U. S. Geological Survey, Denver, Colorado.



SKETCH COPIED FROM MacDONALD NOTES-1961

LANAI AIRPORT BASE

LANAI INN-AUXILIARY BASE

FIG. 1. Sketch showing locations of two gravity base stations on Lanai, Hawaii, used in this preliminary survey.

the assumption that bulk density above sea level was 2.3 g/cc. Because of the accumulation of low density material at the surface, an elevation correction factor of 0.0695 mgal/ft was used in reducing Lanai data for the map of Figure 2. This factor corresponds to a density of 2.0 g/cc.

Use of 2.0 instead of 2.3 for specific gravity has the result of enhancing the gravity anomaly centered on the Palawai Basin. The 40–60-mgal Bouguer anomaly over the assumed center of volcanism is a prominent feature of the gravity fields of other Hawaiian volcanoes (Kinoshita et al., 1963). The 40-mgal anomaly centered on the Palawai Basin is the major gravity feature on Lanai. The geological interpretation of Stearns (1940) suggests that the Lanai plateau and its contemporary depressions are the remains of the ancient center of volcanism for Lanai Volcano. The gravity interpretation tends, therefore, to confirm the geologic one.

IMPLICATIONS OF THE LANAI BOUGUER ANOMALY

Figure 2 shows the well-defined Palawai anomaly. The gravity ridge to the northwest indicates the possibility of an ancient rift in that direction. There is less control to the southeast where another rift zone could possibly exist. From R-10 and R-4 one gets a wonderful view of the scenery; but these stations are poor from the point of view of near-station elevation change. Whereas other stations along the beach or on the plateau get terrain corrections of less than 1 mgal, computed terrain corrections for stations on the mountain go from 5 to 15. And in some cases they would be even higher were the terrain variations fully known and accounted for. Thus R-4 and R-10, as plotted, represent idealized Bouguer anomalies which contain very liberal terrain corrections. Stations along the eastern shore of Lanai would be especially useful in delineating any east-west gravity trend not clarified by the present coverage. Such additional coverage is suggested, as well as possible additions on and around the northwest lobe of Lanai.

ACKNOWLEDGMENTS

We are grateful to William Aldrich, Dole Plantation Manager, for permission to use Dole's rain gauge data and field maps. Adolph H. Desha, Dole Field Superintendent, was most generous with his time, advice, and engineering data. He has since been kind enough to

TABLE 1  
READINGS AT LANAI INN,  
CORRECTED ONLY FOR TIDAL EFFECT

DATE	TIME	READING (mgal)
12-27-62	13:16	2472.43
12-27	16:11	2742.49
12-27	18:18	2472.53
12-28	07:40	2472.55
12-28	18:10	2472.58
12-29	08:30	2472.64
12-29	11:58	2472.48
12-29-62	13:25	2472.54



# A Gravity Survey of the Island of Kahoolawe, Hawaii<sup>1</sup>

AUGUSTINE S. FURUMOTO

THROUGH THE COURTESY of the U. S. Marine Corps, a gravity survey of the island of Kahoolawe was conducted in the spring of 1964. Pre-selected points on the island were visited by means of a helicopter, operating from Kaneohe Marine Corps Air Station, and gravity readings were taken. On the way to Kahoolawe and on return, stops were made at Kahului Airport on Maui to tie the data into the gravity network of the Hawaii Institute of Geophysics.

The instrument used was the Worden gravity meter with slow drift. Altogether, 15 observations were made on Kahoolawe within a space of 3½ hours. The observation points covered the entire island.

The field data were reduced by applying

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 94.

Bouguer corrections with the assumption of a surface density of 2.3 g/cm<sup>3</sup>. The reduced data were plotted on a map of the island and contours of 5-mgal intervals were drawn. The results are shown in Figure 1. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 5).

A region of high positive anomaly exists on the eastern side of the island. This agrees with surface geology, which shows a center of former volcanic activity on the eastern side of the island.

## REFERENCE

HAWAII INSTITUTE OF GEOPHYSICS. 1965. Data from gravity surveys over the Hawaiian Archipelago and other Pacific islands. Hawaii Inst. Geoph. Rept. 65-4, March 1965. 10 tables.

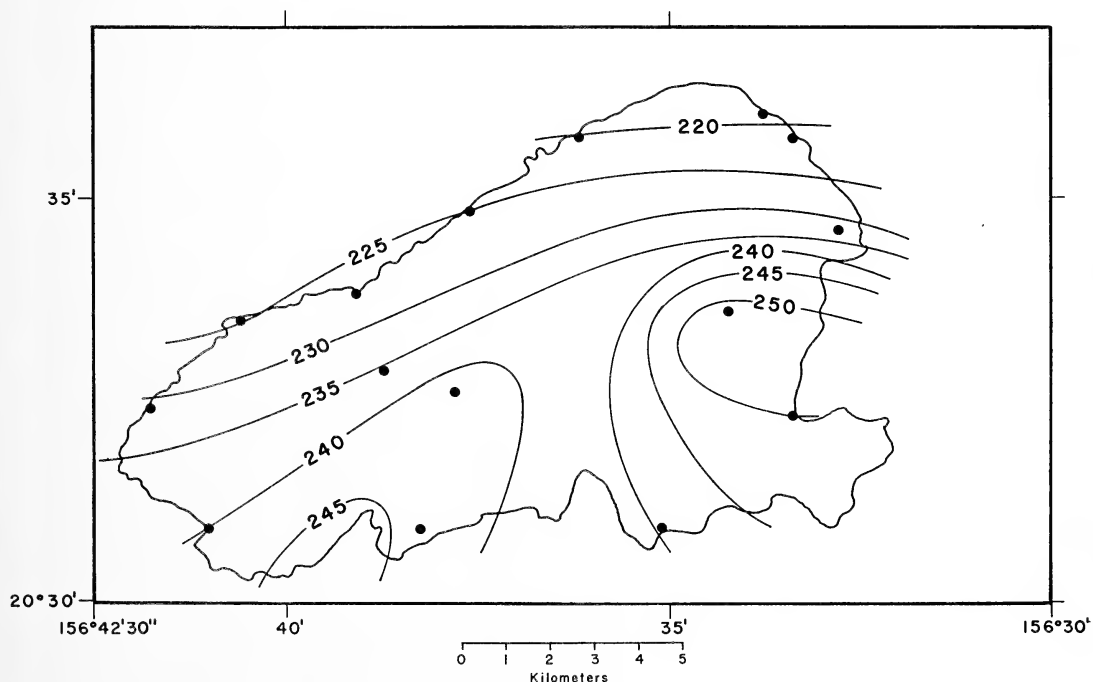


FIG. 1. Bouguer anomaly map of the island of Kahoolawe. Values are in milligals.

# A Gravity Survey of the Island of Oahu, Hawaii<sup>1</sup>

WILLIAM E. STRANGE, L. F. MACHESKY, and GEORGE P. WOOLLARD

PRIOR TO THE PRESENT STUDY four pendulum bases had been established on the island by the U. S. Coast and Geodetic Survey (Duerksen, 1943): (1) a submarine pendulum observation at the port of Honolulu by Vening Meinesz (1934), (2) submarine pendulum observations at various sites at Pearl Harbor by personnel of the Lamont Geological Survey (Worzel, in press), (3) pendulum observations at the Bishop Museum (Woollard and Rose, 1963), and (4) a reconnaissance gravimeter survey at some 30 regionally distributed sites by Woollard (1951). Although personnel of the U. S. Geological Survey and the U. S. Air Force Air Photographic and Charting Survey had also established gravimeter stations in some areas, their data were not generally available.

The present survey was a follow-up on the original work of Woollard (1951), who had shown that the gravity field was characterized by positive Bouguer anomalies ranging from +197 to +309 mgal, and that the maximum anomalies were correlated with two major volcanic calderas over which there appeared to be a local effect of about +110 mgal. Although Vening Meinesz (1941) had concluded that the Hawaiian Islands represented an extra mass on the earth's crust having a density of about 2.94 g/cc, Woollard's analysis of the gravity data suggested a mean density of only 2.3 g/cc and that only the volcanic pipes creating the local anomalies were characterized by a high density.

Inasmuch as in the interim since Woollard's original reconnaissance survey a considerable amount of crustal seismic information had been obtained as well as offshore gravity data, it was decided to make a more complete gravity survey of Oahu which could be analyzed using modern computer techniques. Oahu also constituted the logical place for a meaningful inte-

grated geophysical study of the subsurface mass distribution associated with volcanic calderas in that, through erosion and crustal subsidence, both of the calderas having gravity expression lay essentially at sea level. Thus, there was no significant surficial mass contribution to the anomalies. Other favorable factors associated with Oahu were the road system giving easy access to most of the island, generally good elevation control, the ability to carry out gravity surveys over the center of volcanic pipes without the complications of major elevation changes, and local U. S. Marine Corps helicopter support for making observations in otherwise inaccessible areas. In all, some 512 gravity stations were established; their locations are indicated in Figure 1. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 6). The observations were established by the writers with the assistance of A. S. Furumoto and L. W. Kroenke.

## BASE STATIONS

The base value used was that for Hickam Air Force Base, which had been established originally by Woollard in 1948 and subsequently reoccupied and tied to the Washington national gravity base many times (Woollard, 1950; and Woollard and Rose, 1963). The adopted value for this base on the Potsdam (Bad Harzburg) system is 978.9337 gal. Because Honolulu is used extensively as a control point for all gravity surveys in the Pacific area, and the International Air Terminal is too far removed from Hickam Air Force Base to permit reoccupation of the Hickam base, Woollard had established a number of auxiliary bases (Woollard and Rose, 1963). However, because of new construction most of these base sites can no longer be recovered. The descriptions and values of these earlier bases and of new bases established by the writers are given in the following list. Figure 2 shows the base interconnections.

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 95.



FIG. 1. Bouguer gravity anomaly map of the island of Oahu, Hawaii.

Earlier Gravity Bases

Barbers Point Naval Air Station (WA 442).  
To left of door to Fleet Logistics Air Terminal, Entrance 2.

21°18.9'N  
158°04.5'W      21 ft      978.9720 gal

Hickam Air Force Base (WA 443). In lobby  
of MATS terminal, next to wall map of Pacific Ocean.

21°20.5'N  
157°57.5'W      21 ft      978.9337 gal

Old Honolulu International Airport (WA 444).  
At base of flag pole by Gate 4A, near Medical Inspection Building.

21°19.5'N  
157°55.6'W      13 ft      978.9325 gal

John Rodgers Naval Air Station (WA 445).  
To left of door to Fleet Logistics Air Terminal.

21°19.2'N  
157°55.2'W      6 ft      978.9290 gal

Wheeler Air Force Base (WA 446). At runway 150 ft in front of Hangar 2.

21°29.4'N  
158°02.2'W      824 ft      978.9247 gal

Pendulum Station, Bishop Museum. On ground floor of the Administrative and Research Annex Building, in the north corner of Room 2 at floor level, which is about 3 ft below level of ground immediately outside; 40 ft southeast of northwest wall and 3 ft southwest of northeast wall of building.

21°20.2'N  
157°52.4'W      80 ft      978.9520 gal

New Gravity Bases

New International Airport Terminal. On ground level sidewalk on street side of terminal, alongside right-hand pillar nearest curb when facing up-ramp nearest incoming domestic baggage center (Waikiki end of terminal).

21°20.1'N  
157°55.4'W      11 ft      978.9330 gal

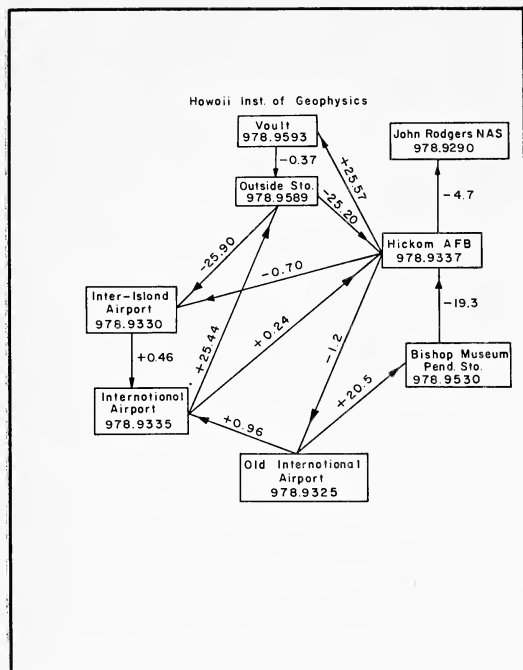


FIG. 2. Local gravity base interconnections, Honolulu, Hawaii.

New Inter-Island Terminal. On concrete sidewalk next to third rock column from Aloha Airlines or fourth rock column from Hawaiian Airlines.

21°20.2'N

157°55.5'W      11 ft      978.9330 gal

Hawaii Institute of Geophysics (University of Hawaii campus). Primary site: in center of flush (floor) pier in basement vault at south-west end of Institute of Geophysics building.

17°30.6'N

157°49.2'W      61 ft      978.9593 gal

Secondary site: on concrete walkway about 1 ft left of doorway leading into Room 108 (when facing door), and about 2 ft to the right of a large stone pillar.

17°30.6'N

157°49.2'W      72 ft      978.9589 gal

#### DETAILS OF SURVEY

The gravity station observations on Oahu were taken with Worden gravimeter No. 607 and Worden gravimeter No. 366. Most of the stations were taken along public streets and

roads, using automobile transportation. Most of the mountain stations were taken at helicopter pads, using helicopter support provided by the Kaneohe Marine Corps Air Station. Certain mountain stations, however, were taken during an overnight foot traverse into the Koolau Range. Except for the foot traverse, readings for drift control were taken at the base station at the beginning and end of each day's work. If possible, reoccupations were made at intermediate times to improve drift control. For the foot traverse the base station tie was made 36 hours after the initial reading. However, overnight drifts were removed by reoccupations and the base tie was used only to remove running drift. Daily drift was normally less than 0.5 mgal per day and, judging from readings taken on the days when intermediate reoccupations were made, assumption of linear drift over an entire day's work seldom produced errors in excess of 0.1 mgal. Elevations were taken from U. S. Geological Survey 7½' quadrangle maps, by reference to sea level along the coast, or, in those cases where bench marks existed, at U. S. Coast and Geodetic Survey bench marks. The accuracy of the elevations is variable. Elevations for stations taken at bench marks or at points where useful elevations were given on the maps are probably accurate to within 1-2 ft. Most of the other elevations for stations lying along public streets and roads are accurate to 10 ft or better. For a few stations greater elevation errors are possible. Elevation errors of up to 20 ft are possible for those stations established by helicopter in areas of the Koolau and Waianae ranges, and elevations for stations established on the overnight foot traverse could be in error by as much as 50 ft. All latitudes and longitudes were taken from the 7½' quadrangle maps and are generally accurate to within 0.1' or better.

#### REDUCTION OF DATA

Normal data-reduction procedures were carried out for the data, with corrections made for drift and earth tides. The meter constant for meter No. 607 was 0.11457 mgal per scale unit and that for meter No. 366 was 0.050637 mgal per scale unit. Comparisons of these meters against the pendulum stations of the west-

ern North American calibration line and intermediate stations established with other gravity meters and comparisons against other meters on the mid-Pacific calibration line indicate that gravimeter No. 607 has a screw effect which causes the calibration constant to vary from 0.1140 to 0.1150 mgal per meter unit for different ranges of the gravimeter. The exact nature of this screw effect has not been definitely established, but since the error to be expected from this source would generally be 0.2 mgal or less no attempt was made to take it into account in the reductions. The screw effect in gravimeter No. 366 was small and did not exceed 0.1 mgal.

Terrain corrections were carried out where it was believed that the effect would be larger than 1–2 mgal. Two different methods were used—the normal circular template method and a profile angle method. The profile angle method is only approximate and the complete Bouguer anomalies obtained by this method may be in error by 1–2 mgal. The simple Bouguer anomalies for most of the stations are probably accurate to better than 1 mgal. A few of the stations where elevation control is uncertain may be in error by as much as 5 mgal.

No detailed interpretation of results will be given here, but a few brief comments can be made. The Bouguer gravity anomaly on the island of Oahu varies from a low of about  $-190$  mgal to a high of about  $+310$  mgal. The lowest value occurs in the Pearl Harbor area and perhaps is caused partly by the thick section of sediments present. The highest values are associated with the Koolau and Waianae volcanic calderas as defined geologically. Positive anomalies of 115 mgal magnitude are associated with each of these calderas. The major northwest rift zone of the Koolau volcano and the south and northwest rift zones of the Waianae volcano have lower gravity positive anomalies associated with them and average  $+50$  mgal above the general level. As seen from the Bouguer anomaly map (Fig. 1), the topographic effect of the island is not pronounced because the gravity effect of the two major volcanic pipes and their associated rifts dominate the gravity field. Also, it is to be noted that al-

though Salt Lake Crater, where inclusions of eclogite are common, has a small gravity effect of about 5 mgal, other late-stage volcanic centers, such as Diamond Head, Koko Head, and Punch Bowl, have no discernible gravity effect. This implies no density-significant contrast between the pipe filling and the surrounding lavas.

#### ACKNOWLEDGMENTS

We would like to acknowledge the excellent cooperation of the U. S. Army, Navy, Air Force, and Marine Corps, who provided permission for establishment of gravity stations on their installations and often provided special escorts and transportation. The Marine Corps also provided helicopters for establishment of gravity stations in some of the more inaccessible areas in the Koolau and Waianae ranges. The work was carried out under NSF Grant No. GP2256 under the over-all supervision of Dr. G. P. Woollard.

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# A Reconnaissance Gravity Survey of the Island of Kauai, Hawaii<sup>1</sup>

HAROLD L. KRIVOV,<sup>2</sup> MELVILLE BAKER, JR., and EUGENE E. MOE<sup>3</sup>

**ABSTRACT:** A large Bouguer anomaly on Kauai, similar to anomalies found at most of the other major volcanoes of the Hawaiian Islands, lies about 10 miles east of the caldera indicated by geologic mapping. Another gravity high suggests a second center of volcanism just west of the island.

Average Bouguer values on Kauai are higher than on other Hawaiian islands, indicating either that the crust beneath Kauai is 1–2 km thinner than it is beneath the eastern part of the Hawaiian Chain, or that the zone of increased density in the dike complex lies closer to the surface at Kauai than do similar cores within other islands of the chain.

BETWEEN THE 26TH AND 30TH of May, 1963 the authors carried out a reconnaissance gravity survey of the island of Kauai in Hawaii. Stations occupied are shown in Figure 1, a generalized topographic map of Kauai. A large part of Kauai is rugged and inaccessible, and in the course of this preliminary survey most available roads were traversed. A more complete picture of the gravity field of Kauai must await further penetration of the island with meters carried by helicopters, boats, and ground parties.

The present gravity survey was planned to take advantage of the availability of a LaCoste and Romberg geodetic gravity meter and of recently completed topographic mapping on Kauai. The results are intended to supply a general idea of the local gravity configuration on Kauai, to permit comparison of the gravity field on Kauai with that on other islands of the state of Hawaii, and to serve as a guide for further investigations.

## OPERATIONAL DETAILS

The Kauai gravity net was carried from bases on Hawaii, Maui, and Oahu. A new primary base was established at Lihue Airport; the instrument was read directly in the center of a rectangular cement pad used by the U. S. Weather Bureau as a theodolite base. This pad is between the airport terminal building and

the weather dome. A secondary base was established on the ground near the front steps of the Lani Motel in Lihue. Tentative base values, tied to G. P. Woollard's base (personal communication) at the old International Air Terminal, Oahu, are as follows:

STATION	GBV
Lani Motel	979,044.3
Lihue Airport	979,037.2

Table 1 lists repeat readings made at Lani Motel during this survey. The negligible diurnal drift, as well as the small total drift in the 5-day period, provide confidence for the zero-drift treatment accorded data collected in any single day. The repeat readings in Table 1 have been corrected for tidal attraction according to Goguel (1962).

The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 7).

TABLE 1  
REPEAT READINGS MADE AT LANI MOTEL,  
LIHUE, KAUAI

DATE	TIME (HST)	READINGS (mgal)
5/26/63	18:28	2690.66
5/27/63	07:16	2690.64
5/27/63	20:27	2690.69
5/28/63	07:09	2690.77
5/28/63	20:00	2690.60
5/29/63	07:35	2690.75
5/29/63	19:37	2690.74
5/30/63	08:10	2690.75

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.

<sup>2</sup> U. S. Geological Survey, Denver, Colorado.

<sup>3</sup> U. S. Geological Survey, Kauai, Hawaii.

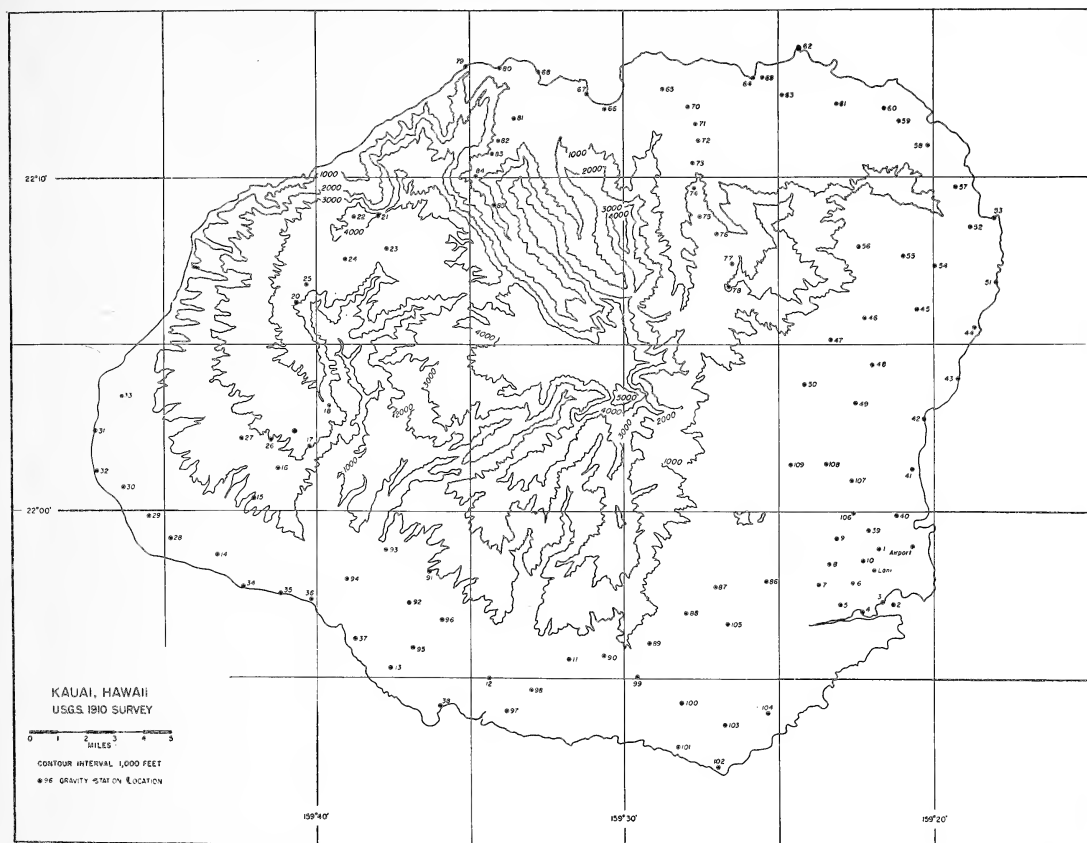


FIG. 1. Topography of Kauai, Hawaii, showing gravity meter stations.

Stations were selected and located on U. S. Geological Survey 7½-minute compilation prints with a scale of 1:24,000. Figures 1 and 2 are based on existing U. S. Geological Survey 1:62,500 maps of Kauai, to which station locations were transferred for greater convenience.

#### DETAILS OF INTERPRETATION

For ease in comparing results of this survey with those of previous Hawaiian surveys, the Bouguer anomalies are based on a combined elevation correction using 2.3 as bulk density down to sea-level. The use of density 2.3 has been discussed by Woollard (1951) for Oahu gravity and by Krivoy and Eaton (1961) for the gravity of Kilauea volcano on Hawaii island. As the gravity survey extends westward from the fresh, vesicular, and relatively uniform flows of Hawaii toward the more deeply weathered older islands of the state, the choice of 2.3 dens-

ity remains convenient albeit less defensible. Not much is known about the extent to which the more deeply weathered islands are mantled by soil and saprolite with density as low as 1.0. Soil conservation studies, where they have been made, habitually are concerned with only the first few feet of soil-cover—the zone of interest in agriculture and in erosion studies. Kauai, therefore, may be largely overlain by varied erosional products with densities much less than 2.3. Macdonald et al. (1960) describe the deep weathering and the vegetative cover on Kauai which make determination of strike and dip impossible in most places.

It should be noted that assuming too high a density for the lavas of Kauai would result in a Bouguer configuration which undervalued high elevation stations. Thus, the unusually high Bouguer anomalies mapped in Kauai would be even larger if a more realistic (smaller) density value were known and were applied.

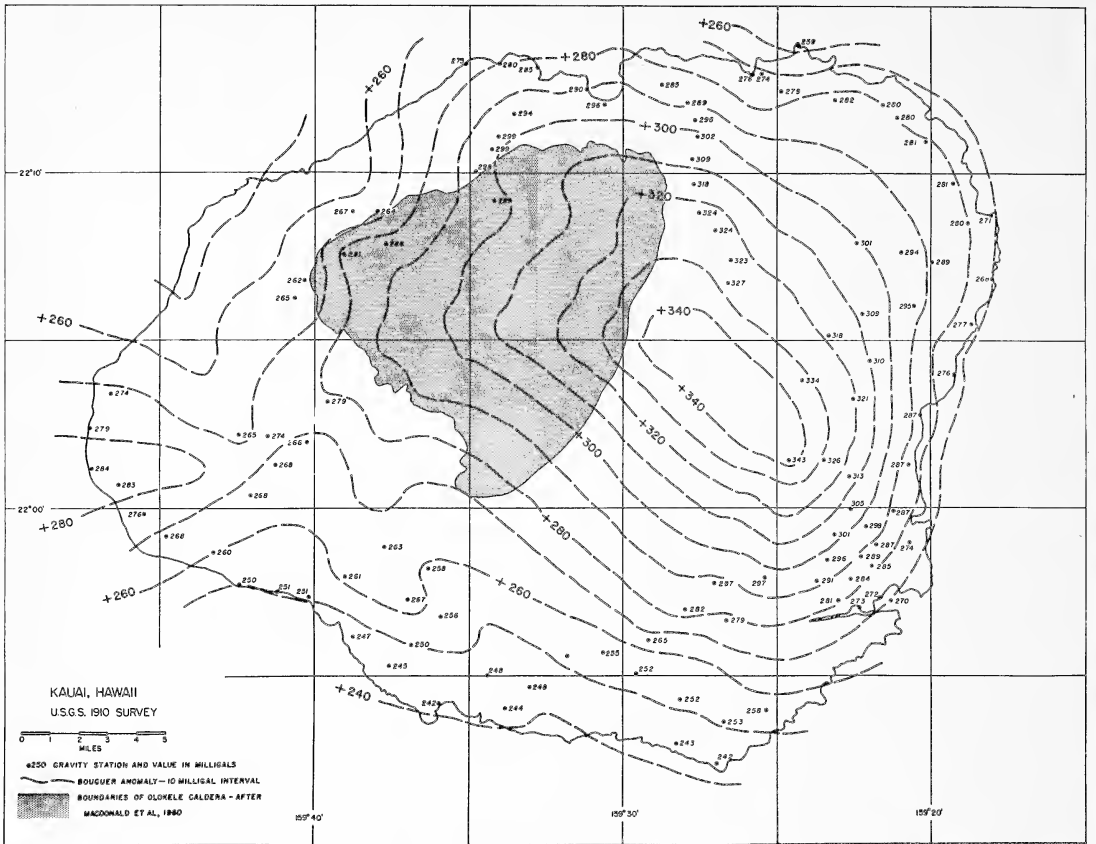


FIG. 2. Bouguer anomaly map of Kauai, Hawaii, showing station values based on 2.3 density. No topographic corrections have been included.

### IMPLICATIONS OF THE BOUGUER ANOMALY MAP (FIG. 2)

Gravity work by Woollard (1951) on Oahu and by Krivoy and Eaton (1961) at Kilauea clearly indicates that Hawaiian volcanoes display distinctive Bouguer gravity highs which appear to be associated with their centers of volcanism. Work by Kinoshita et al. (1963) upon Kohala, Mauna Kea, and Mauna Loa on the island of Hawaii bears out the earlier indications; and unpublished studies by Krivoy and Kinoshita show diagnostic highs for Mauna Loa on Molokai, for Palawai Basin on Lanai, and for Haleakala on Maui.

Local Bouguer anomaly highs of approximately 70 mgal are centered on currently active Hawaiian volcanoes. In the cases listed above for Oahu, Hawaii, Maui, Lanai, and Molokai, the Bouguer highs coincide with major centers

of volcanism, as revealed by topographic and geologic evidence. In two interesting examples, Koolau on Oahu and Kohala on Hawaii, the Bouguer high is displaced from the topographic high. At Koolau erosion and/or faulting have removed the original topographic high over the central volcanic complex, the highest remaining portion of the shield being its southwestern flank. The Bouguer high is centered on the eroded, low-lying dike complex. At Kohala the Bouguer high is displaced southeastward from the present summit. Possibly it reveals the dense central part of an ancestral Kohala shield that was buried by flows from the younger Mauna Kea volcano.

On the island of Hawaii (Kinoshita et al., 1963), terrain corrections were computed out to zone N (Hayford-Bowie). They provided large corrections—as much as 50 mgal—for

stations on the rather steep Mauna Kea. The gravity configuration over the low shield volcano Kilauea, however, was only slightly modified by consideration of terrain both on land and off-shore. The more subtle gravity anomalies, such as those on Mauna Kea and Mauna Loa, were "improved" by the addition of terrain correction, albeit this was in a direction which emphasized correlation between gravity and topography. Strong gravity features, such as the Kohala and Kilauea anomalies, were increased in size and gradient but were not seriously displaced in the final terrain-corrected product. On Hawaii, for example, stations at the Bouguer high on Kohala volcano received less than 6 mgal of terrain correction. Stations on Kilauea received less than 5 mgal. The major Kauai Bouguer anomaly, in this same sense, would be augmented but not seriously shifted.

Figure 2 shows the location of gravity stations and the Bouguer value for each on the island of Kauai. It also shows the location of the Olokele caldera mapped by Stearns (1946) and by Macdonald et al. (1960). Macdonald et al. (1960:32-33) state that "the major caldera of the Kauai shield" is "twice the size of Mokuaweoweo on Mauna Loa . . . but its boundaries are not accurately known." The Bouguer high, as mapped and contoured on Figure 2, does not coincide with the caldera inferred from geologic data. The 340-mgal high is centered about 10 miles east of the center of Olokele caldera. If the relations are similar to those of the other Hawaiian volcanoes studied, the gravity high outlines the most persistent source of lava responsible for building the Kauai shield and probably the caldera site, but the exact relationship between Bouguer high, topographic high, and mapped caldera complex requires further study.

The absence of a gravity nose extending from the gravity high, such as that along the east rift zone of Kilauea, is in agreement with the absence of any marked submarine ridge radiating outward from the island in that direction.

A second anomaly on Kauai is the west-trending high which emerges on the west side of the island. Mapping by Stearns (1946) suggests that a center of volcanism was once active and formed the elongate ridge presently sur-

mounted by Niihau, the island just west of Kauai. Macdonald et al. (1960) show many dikes in west Kauai which could be an extension of a Niihau volcanic center. It should be possible to clarify the situation with additional gravity measurements, mainly on Niihau. However, because of the angle between the two elongate Kauai gravity highs as presently mapped, it does not seem likely that they relate to branches of a single volcanic system. Rather, it would appear that they point to an intergrowth of two distinct volcanoes.

#### LOCAL GRAVITY FIELD

Woollard (1951) offered the first complete interpretation of the gravity field of one of the Hawaiian Islands (Oahu). In this perceptive paper he described the probable source of the Waianae and Koolau gravity highs as the intrusive complexes which mark their volcanic centers. This interpretation has been confirmed by recent studies of the gravity fields of active Hawaiian volcanoes (Kinoshita et al., 1963). An additional mass excess may be provided by deeply ponded dense caldera fill. The juxtaposition of intrusive complexes and caldera fill with density as great as 3, and of clinkery or scoriaeous flow basalts with density of about 2.3, may produce the observed Bouguer anomaly.

#### REGIONAL GRAVITY FIELD

If Figure 2 is compared with the published Bouguer anomaly maps of Kilauea, Kohala, Mauna Loa, Mauna Kea, Koolau, and Waianae, a striking difference is readily apparent. Kauai Bouguer values, both high and low, are 20-25 mgal greater than are corresponding highs and lows on the volcanoes listed.

Woollard and Strange (1962) offered important data which bear on the gravity configuration of the Pacific Basin. With an assumption of 0.4 density contrast between crust and mantle, Kauai's gravity (high as compared with the other volcanoes mentioned) could be explained by up-warping and crustal thinning of 4,000-5,000 ft. If the same density contrast is as great as 0.7, crustal thinning could be less than 3,000 ft.

The Bouguer increase might be due also to a larger and/or more dense dike complex at

the seat of Kauai volcanism than is present beneath the other volcanoes.

Geologic intuition leads to the conclusion that the Hawaiian Chain is growing toward the southeast. Younger islands such as Hawaii and Maui are thought to be undercompensated. Conversely, older islands might be expected to be in better adjustment. Were all other factors equivalent, this would yield lower Bouguer values on Kauai—actually the reverse of our findings.

No one has suggested that some of the older islands might be emerging due to erosional stripping. This would involve the mechanism of crustal thinning and would explain an increased Bouguer field.

As another alternative, it is conceivable that Kauai (as are the other islands) is still undercompensated, but that it erupted and grew on the ocean floor in a region of inherently thinner crust.

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# A Gravity Survey of the Island of Niihau, Hawaii<sup>1</sup>

HAROLD L. KRIVOV<sup>2</sup>

**ABSTRACT:** Gravity data collected on Niihau support geologic evidence that the island is an erosional remnant of a dead shield volcano whose center of volcanism was just east of the present Niihau highlands. Bathymetric and gravity evidence offer clues to a genetic link between Niihau and west Kauai; onshore gravity suggests a continuous Bouguer high connecting the two regions. This link would be in accord with ocean-bottom topography, which shows a prominent ridge rising above sea level at Niihau and at Kaula Rock to the west.

A GRAVITY SURVEY of the island of Niihau, Hawaii, was made December 10–12, 1963. It is a pleasure to acknowledge the logistic support, the check of place names, and the hospitality of Aylmer Robinson, Manager, Niihau Ranch. Without his interest this work would not have been possible. I am indebted also to Niihau residents Melvin Pahulehua, Gilbert Pahulehua, Jr., Jacob Kanahele, and Keoki Keamoai, who helped me reach the station sites on Niihau.

Stations were selected by use of the existing 1929 U. S. Geological Survey topographic sheet to determine their elevations. Because of the somewhat generalized character of this map, elevations at many stations may be in error by as much as 20 ft. Such an error in elevation would lead to an error of about 1.4 mgal in the Bouguer anomaly, if we assume a density of 2.3 g/cm<sup>3</sup> for island rocks down to sea level. This basic uncertainty of exact elevation made it superfluous to consider other, much smaller, variables. Thus, I did not make corrections for tidal gravity changes or for meter drift. The latter correction, however, would have been especially small because of the accuracy of the LaCoste and Romberg low-drift portable gravity meter used in this survey. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 8).

Despite its rather small land area Niihau exhibits a large positive Bouguer anomaly similar to those anomalies found on other Hawaiian

volcanoes. A linear high, outlined by the 280-mgal contour, crosses Niihau in a direction N 70° E (Fig. 1) approximately parallel to the submarine ridge which joins Niihau, Kauai, and Kaula (Stearns, 1947: Fig. 3). A 280-mgal high also enters Kauai (Krivoy et al. p. 354 in this issue) from the direction of Niihau, but no gravity data are available over the submarine ridge between Kauai and Niihau.

Geologic mapping indicates that Niihau is a remnant of an ancient volcanic shield which had its center offshore east of the highlands (Stearns, 1947; Macdonald, 1947). The gravity map (Fig. 1) supports this interpretation. Comparison of the gravity field of Niihau with the fields of other, less dissected Hawaiian volcanoes (Kinoshita et al., 1963) suggests that the original volcanic center of the Niihau volcano is close to its eastern shore. Kilauea and Mauna Loa have their centers of volcanism within 10 miles of the 280-mgal contour on their flanks or rifts. An offshore gravity survey between Kauai and Niihau would be of interest because it might delineate the central portion of the original Niihau volcano and clarify the relation between Niihau and west Kauai.

The N 70° E trend of the Kaula-Niihau-west Kauai ridge (Stearns, 1946: Pl. 1) is perpendicular to the northwest trend of the main Hawaiian ridge. Recent bathymetric surveys (U. S. Navy Hydrographic Office, 1961) have detailed a system of topographic lineaments which give the appearance of having been parted by the growing Hawaiian ridge. These lineaments trend N 70° E to N 80° E, about parallel to the Kaula-Niihau-west Kauai ridge.

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.

<sup>2</sup> U. S. Geological Survey, Denver, Colorado.

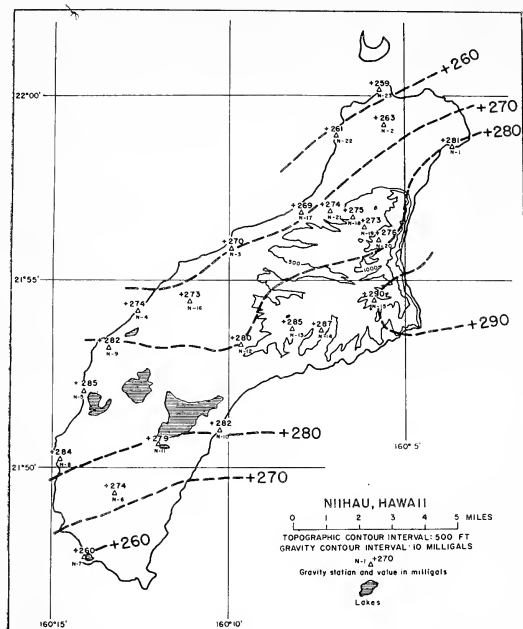


FIG. 1. Bouguer anomaly map of the island of Niihau, Hawaii.

West of the Hawaiian ridge it is possible that these lineaments have been covered by sediments; magnetic anomalies (U. S. Navy Oceanographic Office, 1962) suggest that they do exist, as geophysical expressions if not topographic ones.

Bathymetric data, as well as geomagnetic data from sea-borne surveys demonstrate a remarkable linear pattern of folding or faulting which seems to be a fundamental characteristic of the floor of the Pacific Ocean. This pattern is clear in the northeastern Pacific, but is confused elsewhere by the growth of volcanic chains. In the area of the Hawaiian Islands a

line of growing volcanoes is covering the pre-existing ocean floor with its eroded and extruded products. The Kaula-Niihau-west Kauai volcanic group, although associated structurally, chemically, and generically with the younger volcanoes to the southeast, seems—by virtue of its strike—to be controlled by the confluence of recent tectonism with earlier structure.

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# Gravity Investigations on the Leeward Islands of the Hawaiian Ridge and Johnston Island<sup>1</sup>

LOREN W. KROENKE and GEORGE P. WOOLLARD

THROUGH THE COURTESY of the U. S. Coast Guard, who allowed the senior author to accompany the U. S. C. G. Cutter "Plaintree" during a base resupply cruise in 1964, it was possible to visit many of the small islands and atolls along the Hawaiian Ridge extending from Nihoa to Midway, as well as Johnston I., to make gravity observations. In all, 133 gravity stations were established on Nihoa, Laysan, Lisianski, Pearl and Hermes Reef, and Midway, and twenty-three stations were established on Johnston I. All the leeward islands in the eastern half of the Hawaiian chain consist of volcanic peaks. On the chain's western end, most of the peaks are capped by coral reefs to form atolls. Although single gravity observations had been made on many of these islands by the Air Force Air Photographic and Charting Service, and some were studied as early as 1948 (Woollard, 1950), the present series of measurements are the first to give a sufficient number of observations for a realistic appraisal of the anomaly field, in terms of both the absolute Bouguer anomaly values and the local gravity gradient.

All observed gravity values were referred to the absolute gravity base at the Hawaii Institute of Geophysics established by Woollard (unpublished), and were adjusted for instrumental drift through Woollard's airport gravity bases at Midway I. and Johnston I. (Woollard and Rose, 1963). The observations were made with a low drift-rate Worden gravimeter having a range of 2000 mgal. The reliability of the values is not uniform and may be no better than  $\pm 2$  mgal in the observed gravity values for the central area representing the area of poorest control. Elevations except for those for Nihoa were estimated in most cases by visual observation of sea level and are believed accurate to within  $\pm 2$  ft. Elevations for Nihoa

were estimated from an elevation contour map with 100-ft contour intervals and could be in error as much as 30 ft. Bouguer anomalies were computed using a density of 2.3 gm/cc in the reductions. The table of principal facts for all stations is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 9).

## HAWAIIAN ARCHIPELAGO OBSERVATIONS

The bathymetry surrounding each of the islands is similar, with the land surface falling off rapidly to the northeast and southwest and decreasing over submerged shelf areas elongated parallel to the island chain. In general, the islands have a low elevation and are elongated parallel to the direction of the main oceanic current systems. The exception to this generalization is Nihoa I., which has a maximum elevation of 895 ft and a north shore formed by perpendicular cliffs more than 800 ft high. Based on the observed shapes of the gravity anomalies associated with the volcanic centers on the larger islands at the southeast end of the chain, and the observed magnitudes and gradients observed on these smaller islands, estimates of the location of the center of the gravity highs and the maximum Bouguer anomaly values have been made.

### *Nihoa*

This island covers an area of 156 acres. Rough seas and a landing site rimmed by sea-cliffs made landings from a small boat hazardous as well as difficult. The rocks are principally olivine basalts occurring as flows or dikes. Because the terrain effect is appreciable and difficult to estimate for stations located along the ridge top near the cliff edge, and as the elevation and meter drift control were weak here, the anomalies may have no better than  $\pm 5$  mgal accuracy. The lowest Bouguer anomaly value of +245 mgal (Fig. 1) is found at the

<sup>1</sup>Hawaii Institute of Geophysics Contribution No. 96.



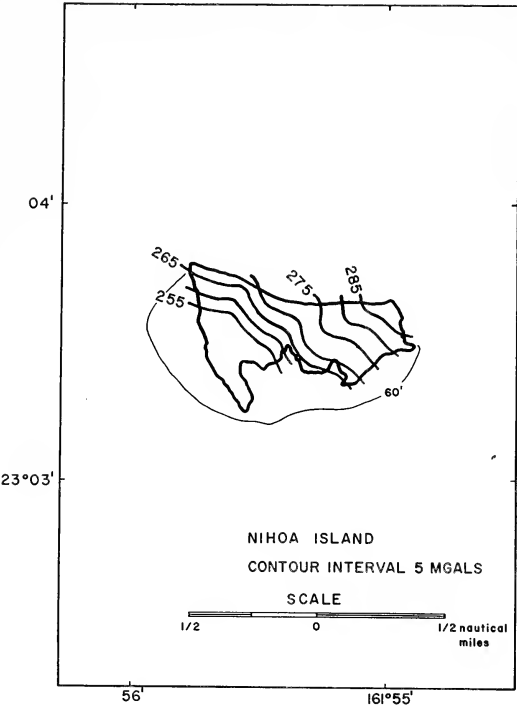


FIG. 1. Bouguer anomaly map of Nihoa I.

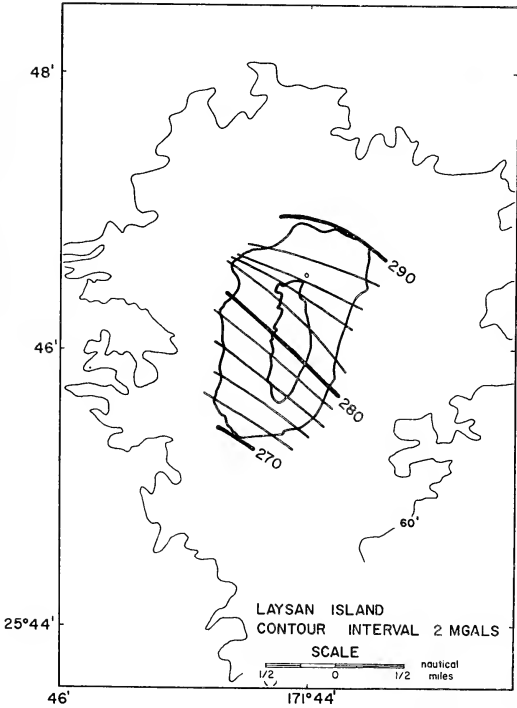


FIG. 2. Bouguer anomaly map of Laysan I.

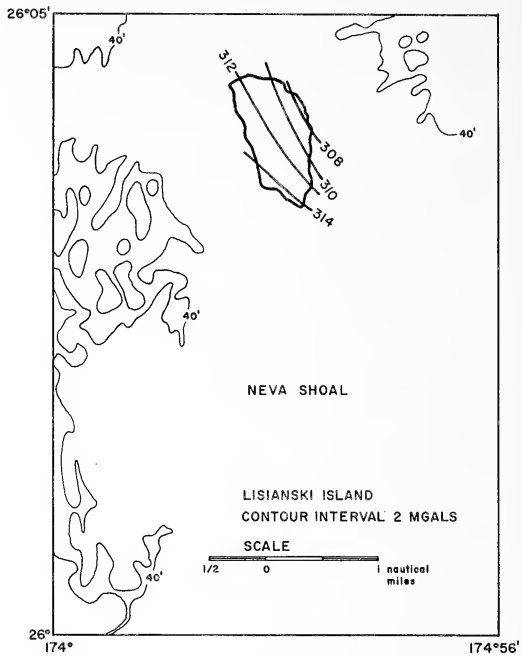


FIG. 3. Bouguer anomaly map of Lisianski I.

southwest corner of the island, and values increase northeasterly to +278 mgal. Based on the observed gravity gradient, the center of the projected gravity high would lie to the north and slightly east of Nihoa and would have an estimated maximum Bouguer anomaly value of +310 mgal.

*Laysan*

The island is rectangular in shape, trending north-south. The Bouguer anomaly contours (Fig. 2) conform to the shape of the island, with the lowest value of +271 mgal located on the south end and the highest Bouguer anomaly of +290 on the north end. The center of the gravity high appears to lie north and slightly east of the land mass. The gravity gradient on the island averages 10 mgal per mile. Assuming that the gradient remains constant, the center of the high will have a value of about +315 mgal.

*Lisianski*

This island is about one-half the width and length of Laysan and is elongated in a north-south direction. The Bouguer anomaly contours (Fig. 3) conform to the island's outline. The

lowest Bouguer anomaly value of +308 mgal was found at the northeast tip, and the highest value of +315 mgal at the southwest tip. The gravity gradient averages 10 mgal per mile and increases towards the southwest. The maximum Bouguer anomaly value at the projected center of the gravity high located to the south and west of Lisianski would be approximately +325 mgal.

*Pearl and Hermes Reef*

This large atoll is comprised of many small islets enclosing a low, coral-filled, shelf area. Only seven of the islets could be occupied, and these are located along the southern edges. A +276 mgal Bouguer anomaly value was ob-

tained on the southeast reef, and values increased to +285 mgal to the southwest. The gravity gradient averages 5 mgal per mile. The contours (Fig. 4) indicate that the high should be found to the north and west of the location of the +285-mgal station, with maximum Bouguer anomaly values possibly as high as +305 mgal.

*Midway*

Midway I. is a large coral atoll. From magnetic and seismic measurements the coral cap is estimated to be 1000–2500 ft thick (Harry Ladd, personal communication). The contoured Bouguer anomaly map (Fig. 5) shows values ranging from a low of +284 mgal on the south

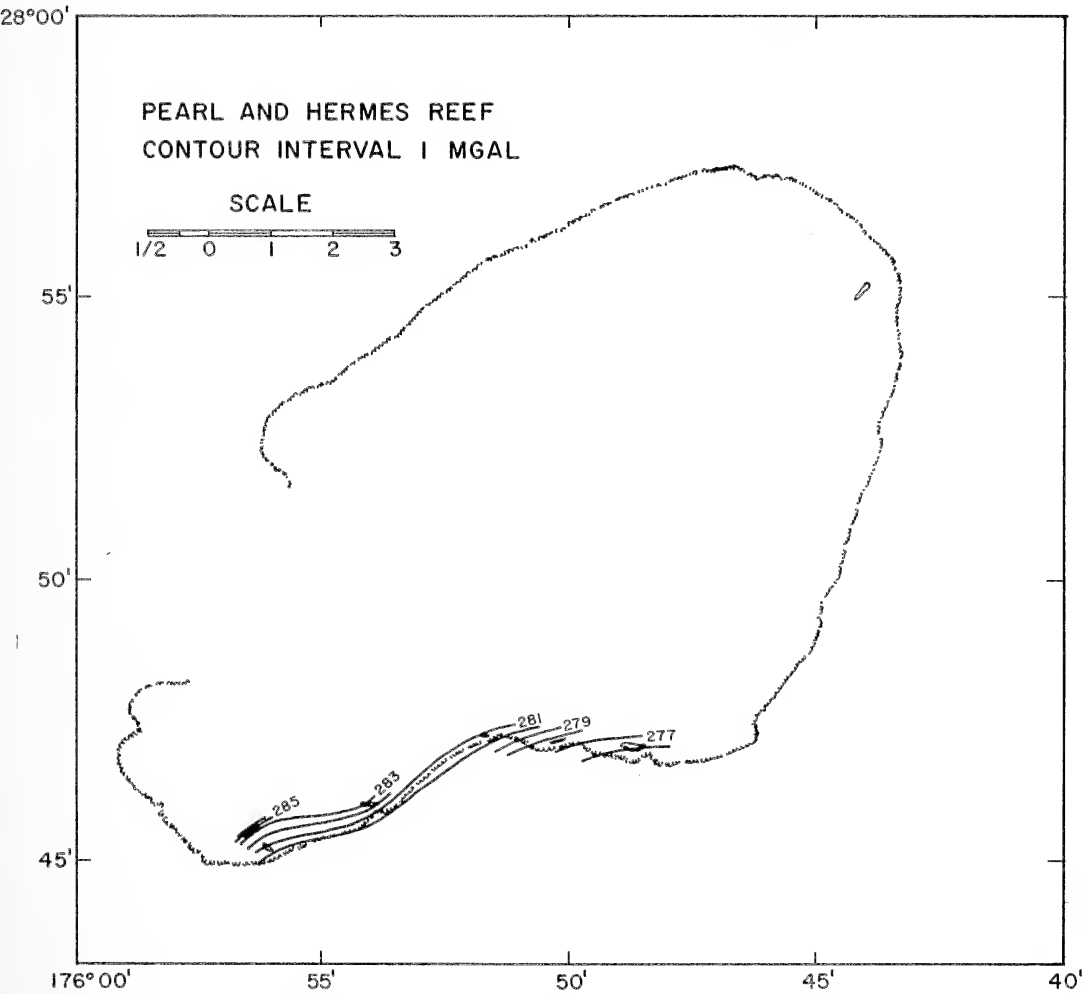


FIG. 4. Bouguer anomaly map of Pearl and Hermes Reef.

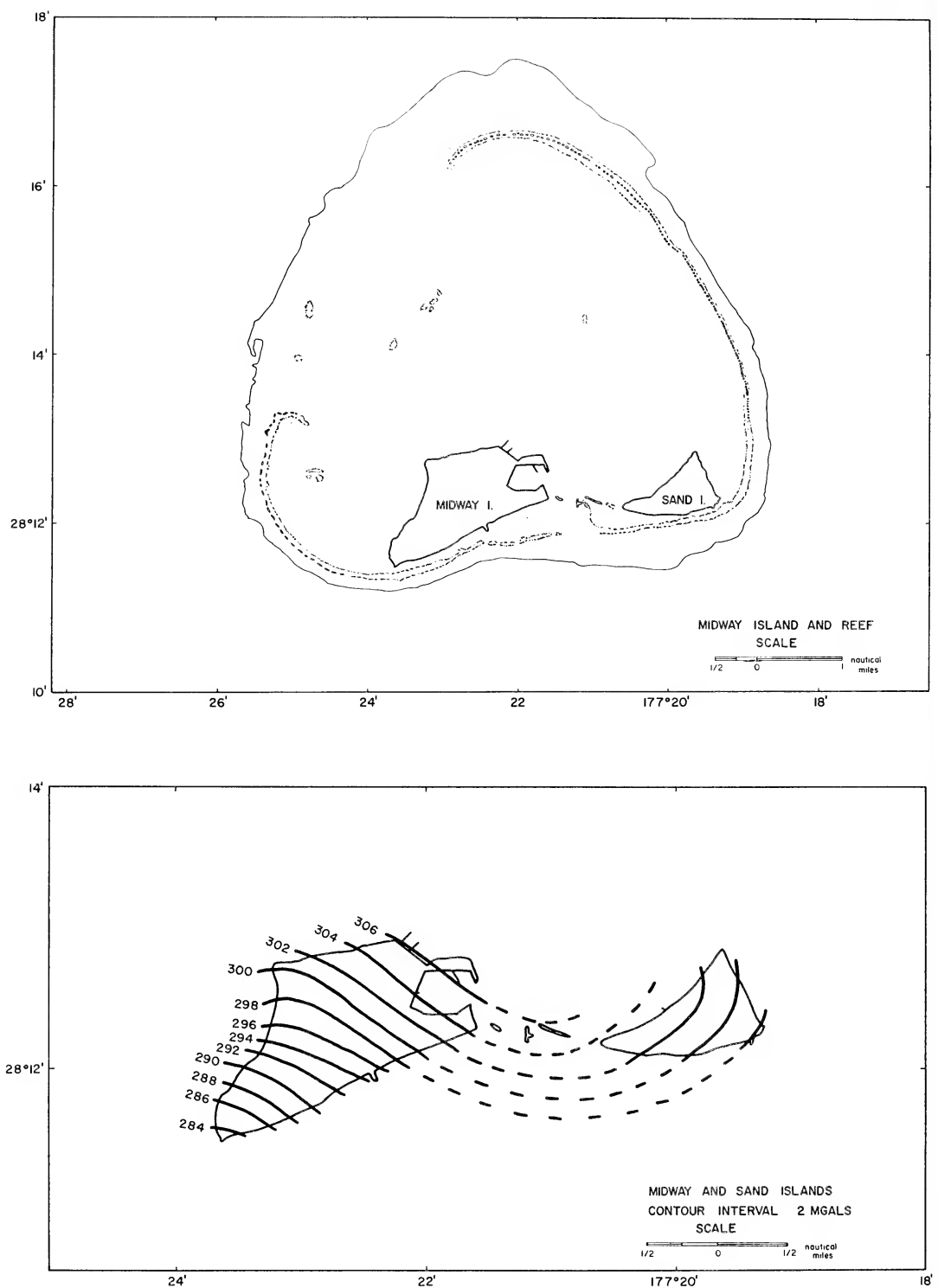


FIG. 5. *Upper*, Midway I. and reef. *Lower*, Bouguer anomaly map of Midway and Sand Is.

of Sand I. to +306 mgal on the north. The gravity gradient on Sand I. averages 10 mgal per mile. The contours indicate a single high with a maximum value of about +320 mgal. The gravity high appears to be positioned midway between Sand I. and Eastern I.

*Johnston*

Located south of Hawaii, at 16°45'N, 169°31'W, Johnston I. is not a part of the Hawaiian Ridge but can be considered geologically as the northernmost of the Line Islands. On the basis of bathymetric contours it appears to lie on the northern end of a continuous shoal area extending southeastward from Johnston I. to Palmyra I. North of Johnston the shoal area has a northeast-southwest trend. Johnston I. itself is elongated in a northeast-southwest direction parallel to the barrier reef that exists to the west and northeast of the island.

As seen from Figure 6, the minimum gravity value of +240 mgal is obtained on the south-

west end of the island and values increase to +251 mgal towards the northeast. Projecting the gravity gradient of 5 mgal per mile would predict a maximum Bouguer anomaly value of +270 mgal at the center of a gravity high lying to the northeast of the island.

SUMMARY

All islands along the Hawaiian Ridge are characterized by high gravity values with Bouguer values approaching +300 mgal, including those islands represented as atolls having a thick coral cap, such as Midway, where an actual value of +306 mgal was observed. All have pronounced gradients of about 10 mgal per mile that appear to be related to a primary volcanic pipe rather than to the topographic configuration. Despite the geologic indications of greater subsidence toward the northwest along the Hawaiian Ridge there is no indication of any systematic change from southeast to northwest in Bouguer anomaly val-

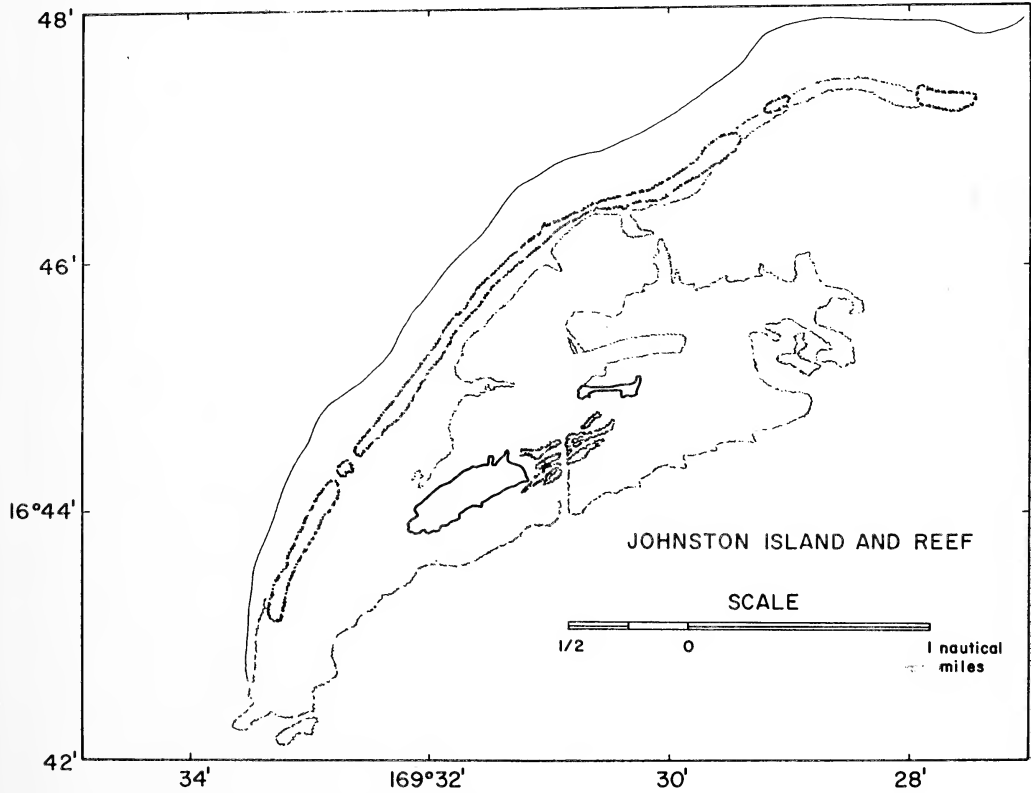


FIG. 6a. Johnston I. and reef.

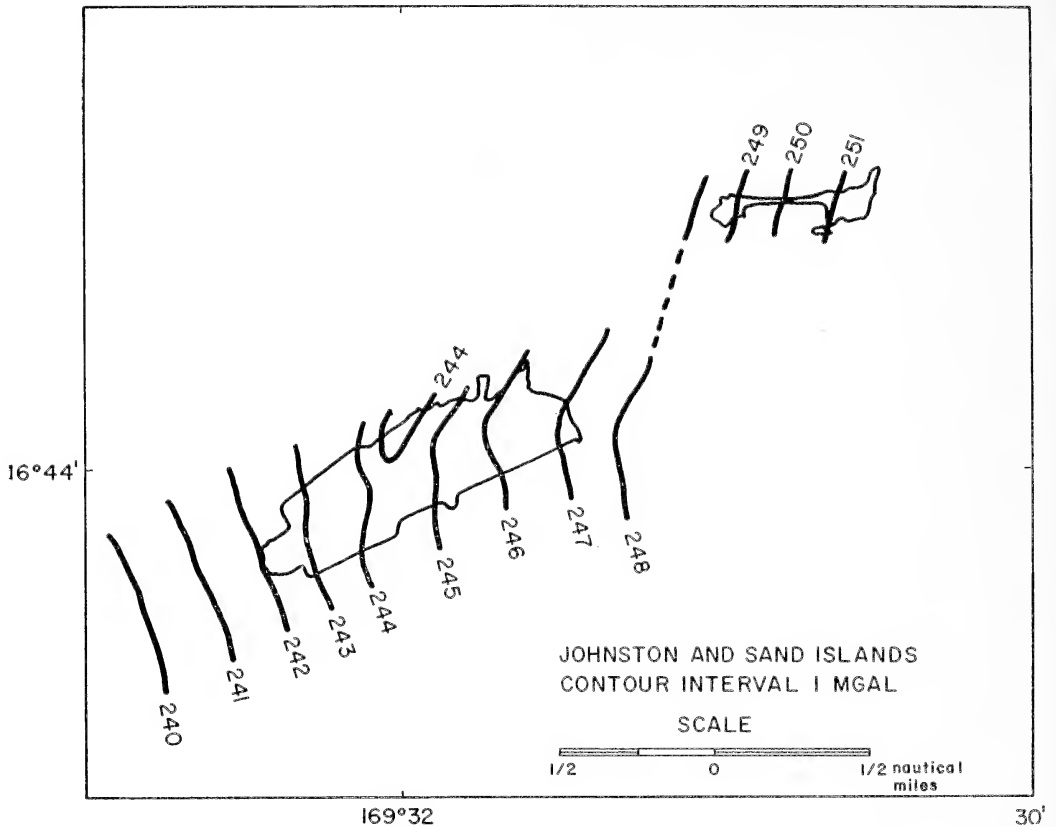


FIG. 6b. Bouguer anomaly map of Johnston and Sand Is.

ues observed on the islands of the Hawaiian group.

Johnston I. has absolute Bouguer anomaly values that are somewhat lower than those of the Hawaiian Islands. These values are intermediate between those found on the Hawaiian Ridge and on the remainder of the Line Islands where R. Mason (personal communication) reports absolute anomaly values ranging from +145 to +175 mgal that can be related to the island platform configuration, with no evidence of a feeder pipe contribution in the anomalies.

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# Gravity Relations in American Samoa and the Society Islands<sup>1</sup>

L. F. MACHESKY

BECAUSE OCEANIC ISLANDS in general have an underlying volcanic platform which can be expected to include a primary feeder pipe containing recrystallized magma, the gravity field observed will reflect both the topographic mass effect of the platform rising from the sea floor and a contribution from the feeder pipe presumably having a filling of denser material. Certainly the early study of Oahu by Woollard (1951) shows that the pipe contribution can amount to more than +100 mgal. To satisfy such a high anomaly requires a density contrast of about 0.5 gm/cc. As there is a geologic restriction on the density of both the platform material and that filling the pipe, one is forced to postulate mantle-like material with a density of about 3.3 gm/cc near sea level in the pipes where such high local anomalies occur. The Bouguer anomaly in such pipe areas often exceeds +300 mgal. If there were no difference between the density of the pipe filling and that of the platform, the anomaly would be only about +200 mgal.

The absolute value of the Bouguer anomaly and the local gravity gradient, therefore, have considerable geologic value, and presumably could be diagnostic in the study of the distribution of tholeiitic basalts, such as are found in Hawaii, and the more alkalic basalts, such as are found in the Society Islands, because there is a significant difference in their respective density values. This is especially important since recent work, such as that of Engel and Engel (1964a, 1964b), has led to the proposal that the major part of all oceanic island platforms is composed of tholeiitic basalt with only a veneer of alkalic basalt on the islands.

To test this hypothesis the writer carried out a series of gravity studies in American Samoa and the Society Islands, where the predominant

lavas at the surface appear to be alkalic basalts, for comparison with the data from the Hawaiian Islands. The table of principal facts is reported elsewhere (Hawaii Inst. Geoph., 1965, Table 10).

## MEASUREMENTS IN AMERICAN SAMOA

The Samoan Islands form a chain trending east to west between 169° and 171° W, at about 14°30' S. They are situated north and slightly east of the Kermadec-Tonga Trench and lie on the oceanic side of the Andesite Line as defined by Macdonald (1949).

From west to east the islands are Tutuila, Ofu, Olosega, and Tau. During July and August 1964, 130 gravity stations were established on these islands, through the use of a Worden gravimeter No. 366. All data are based on the absolute gravity value, at the Hawaii Institute of Geophysics, of 978.9562 gal, as determined by Woollard (unpublished).

### *Tutuila*

Tutuila is the largest island of the Samoan group and covers an area of 54 sq miles. The water increases uniformly to normal oceanic depths north and south of the island, while underwater ridges extend to the east and west. The island is surrounded by fringing coral reefs. Surface geologic investigations show alkalic and tholeiitic basalts, with minor amounts of quartz trachyte and andesite. The highest elevation, atop one of the quartz trachyte plugs, is 2141 ft. A major caldera is situated in the center of the island and extends 6 miles east to west and 3 miles north to south, as determined by Stearns (1944). Well-developed rift zones extend northeast and southwest from the caldera area. The age of the volcanics is estimated to be late Pliocene or early Pleistocene. A brief summary of the geologic history of Tutuila I. as given by Stearns (1944) follows:

<sup>1</sup>Hawaii Institute of Geophysics Contribution No. 97.

1. Outpourings of tholeiitic basalts along a major rift zone.
2. Volcanic activity subsides.
3. Explosive volcanic activity increases with outpourings of andesitic basalts.
4. Collapse and burial of the crater.
5. Period of submergence followed by emergence.
6. Renewed volcanic activity with small outpourings of alkalic basalts to recent times.

The Bouguer gravity anomaly map (Fig. 1) in general corroborates Stearns' conclusions. As the Bouguer anomaly values vary from +233 on the southeast to +293 near the center of the main caldera area, they are very similar to those found in Hawaii. Stearns advocated a single large caldera in the vicinity of Pago Pago, whereas the present gravity survey suggests there may be two separate areas of eruption within the area of this single large caldera. However, because of the ruggedness of the jungle terrain and lack of time, it was not possible to make a firm case for this hypothesis. The secondary caldera proposed by Stearns near the eastern end of the island is not substantiated by the gravity data. However, it is possible that another caldera may occur offshore from the western end of the island. Well-developed rift

zones trending N 60°E and S 60°W are readily apparent from the contoured Bouguer anomaly map. The gravity gradient averages 10 mgal per mile, southwest from the primary caldera, and increases to 20 mgal per mile near the coastline. A low anomalous area is indicated slightly south and east off the east end of the island, and another offshore low is suggested south of the west end of the island. However, their geological significance is not known.

### *Ofu and Olosega*

Together these islands have an area of 3.5 sq miles. They have a bar-bell shape and are separated by a narrow channel that can be waded during periods of low tide. The bathymetry falls off to the north and south, with shallow areas extending east and west of the islands. The highest point on Ofu is 1590 ft, and on Olosega, 2095 ft.

According to McCoy (1965), the predominant exposed rock types are alkalic basalts, and no trachytes are observed. Small exposures of more basic basalts, thought to be more recent in age, also outcrop. It is possible that tholeiitic basalts are present but, if so, they are effectively masked by more recent alkalic volcanics.

Here, as on Tutuila, the gravity data substan-

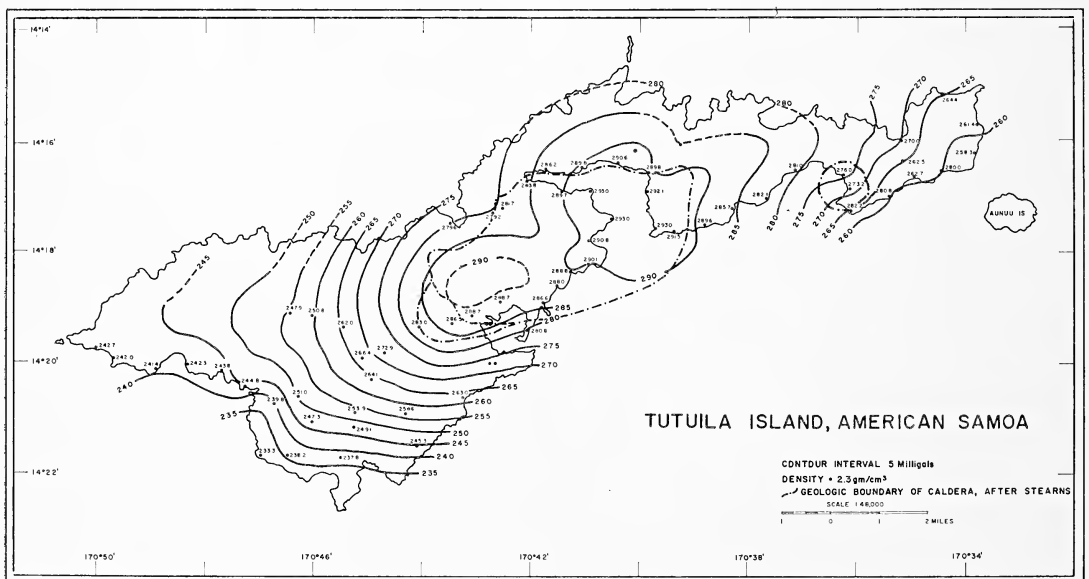


FIG. 1. Bouguer anomaly map of Tutuila I., American Samoa.

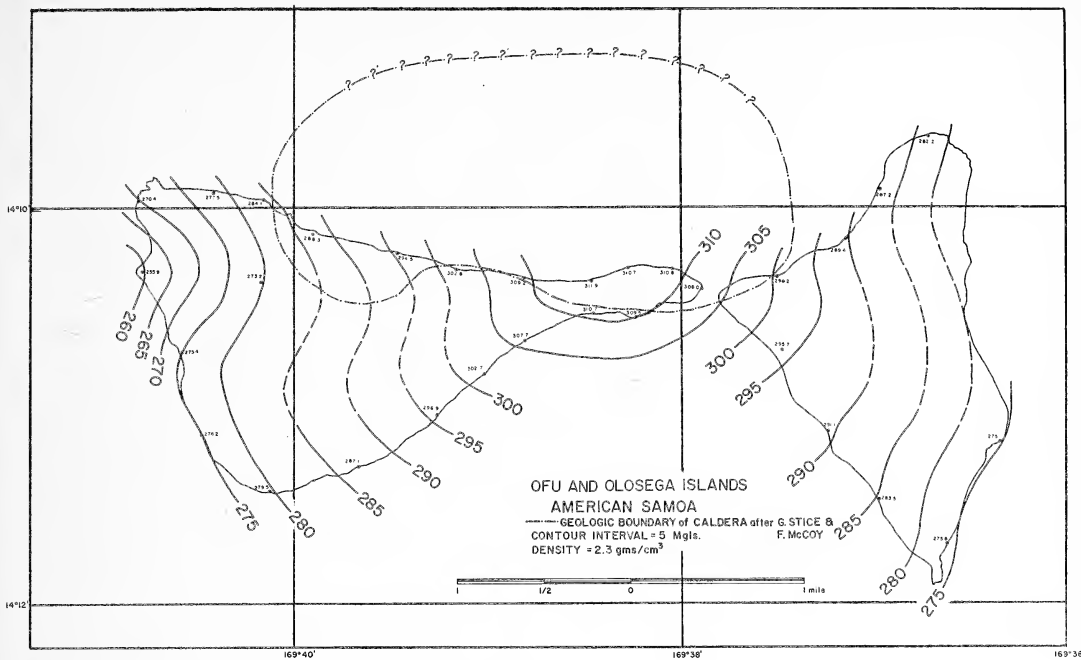


FIG. 2. Bouguer anomaly map of Ofu and Olosega Is., American Samoa.

tiate the geologic information. The gravimetric center of the caldera lying between the two islands (Fig. 2) is slightly east of the geologic center. The major portion of the structure lies offshore to the north of the islands. The Bouguer anomaly contours directly parallel the major rift zones which trend in southwest and southeast directions. The Bouguer anomaly values range from +260 on the east to +312 mgal in the center of the caldera area. A low anomalous area is suggested off the west end of Ofu Island. The maximum observed gradient is 20 mgal per mile. Thus, there is evidence that the island platform mass is tholeiitic basalt and that the feeder pipe contains ultrabasic rock.

*Tau*

Tau has an area of 15 sq miles, and the highest point of 3056 ft is found near the island's center. The water depth increases to the north and south, with a ridge area extending east and west from the land mass. Fringing reefs surround the island. The topography, as on Tutuila, and on Ofu and Olosega, is rugged with precipitous cliffs occurring on the north sides whereas the southern slopes are usually more

gentle. Dense jungle vegetation covers most of the interior, making overland traverses extremely difficult. The geology according to Gary Stice and Floyd McCoy (personal communication) is similar to that observed on Ofu and Olosega. As seen from the northwest, Tau presents a perfect outline of a shield-type volcano.

The Bouguer gravity anomaly map (Fig. 3) depicts a single closure located in the south central portion of the island. The anomaly values vary from +250 to +290 mgal. The anomaly pattern is roughly circular in shape and its center coincides with the caldera which has rift zones extending to the northeast and the northwest from its center. The maximum anomaly gradient of 23 mgal per mile occurs to the north. The gravimetric center of the caldera was not reached, but the maximum anomaly value would appear to be near +300 mgal. Although the geologic indications are that the center of the caldera occurs offshore a short way south of the center of the island, the gravity data suggest that the intrusive center lies directly northward toward the land mass. As on the other islands studied in the Samoan group, the gravity data indicated that the island platform is



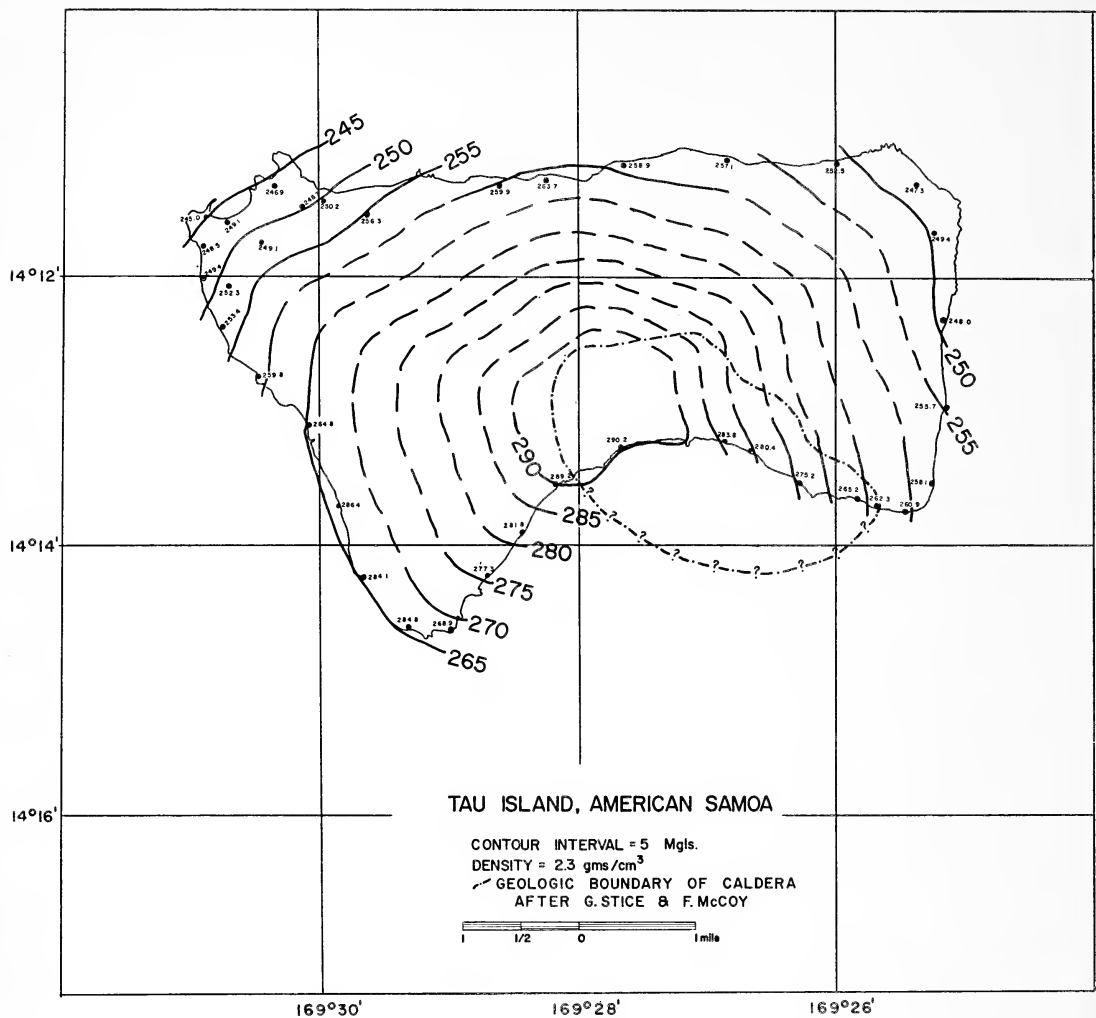


FIG. 3. Bouguer anomaly map of Tau I., American Samoa.

tholeiitic and that the feeder pipe contains ultrabasic rock.

THE SOCIETY ISLANDS

The Society Islands trend in a N 60° W direction and are located between 148° and 152° W and 16° and 18° S. During August 1964, the writer, using a Worden gravimeter No. 366, made 137 gravimeter observations on the islands of Tahiti and Moorea. All gravity data are referred to the absolute value of 978.9562 gal established for the Hawaii Institute of Geophysics gravity base in Honolulu, Hawaii (Woollard, unpublished).

*Tahiti*

Tahiti can be geomorphologically compared with the island of Maui: each is a large, high land mass, connected with a small, lower one by a narrow isthmus. Tahiti-Nui is roughly elliptical in shape, measuring 23 by 18 miles, and is connected by the isthmus of Taravao to the Tairapu Peninsula which is positioned to the southeast of Tahiti-Nui and measures 14 by 9 miles. The highest point on Tahiti is 7339 ft and is located near the geometric center of the island. The highest point on the Tairapu Peninsula is 4341 ft, and it is located near the geometric center of the peninsula. The moun-

tainous and precipitous interior of Tahiti and the complete lack of roads precluded any over-land traverses, hence the present survey was confined to the coastal regions accessible by automobile. Viewed from the northwest, Tahiti presents a perfect shield-shaped structure, similar to the island of Tau, American Samoa.

The island of Tahiti is composed chiefly of alkaline basalts (Williams, 1933). The exposed caldera plug is composed of nepheline monzonites, theralites, and of subordinate nepheline syenites. The geological evidence indicates that a volcanic pipe is located near the geometrical center of Tahiti-Nui. The Taiaapu Peninsula volcanic pipe is geologically defined as being near the center of the peninsula just north of the highest topographic peak. The rock types that form the plug are generally more basic than those observed on Tahiti-Nui, consisting

primarily of essexites and theralites. The original volcanic activity on the Society Islands chain is believed to have originated in the west and migrated eastward. Tahiti is extensively ringed by barrier and fringing reefs.

Although the gravity picture on Tahiti-Nui and the Taiaapu Peninsula is incomplete, due to the absence of data from the interior, the magnitude of the anomalies and gradients observed are diagnostic. The Bouguer gravity anomaly contours on Tahiti-Nui (Fig. 4) outline a circular form with the steepest coastal gravity gradients of 10 mgal per mile occurring in the north half of the island. The size and position of the gravity gradients suggest that the gravimetric center of the caldera will be found slightly north of the geologic position. The observed Bouguer anomaly values range from +180 on the northeast coast to +230

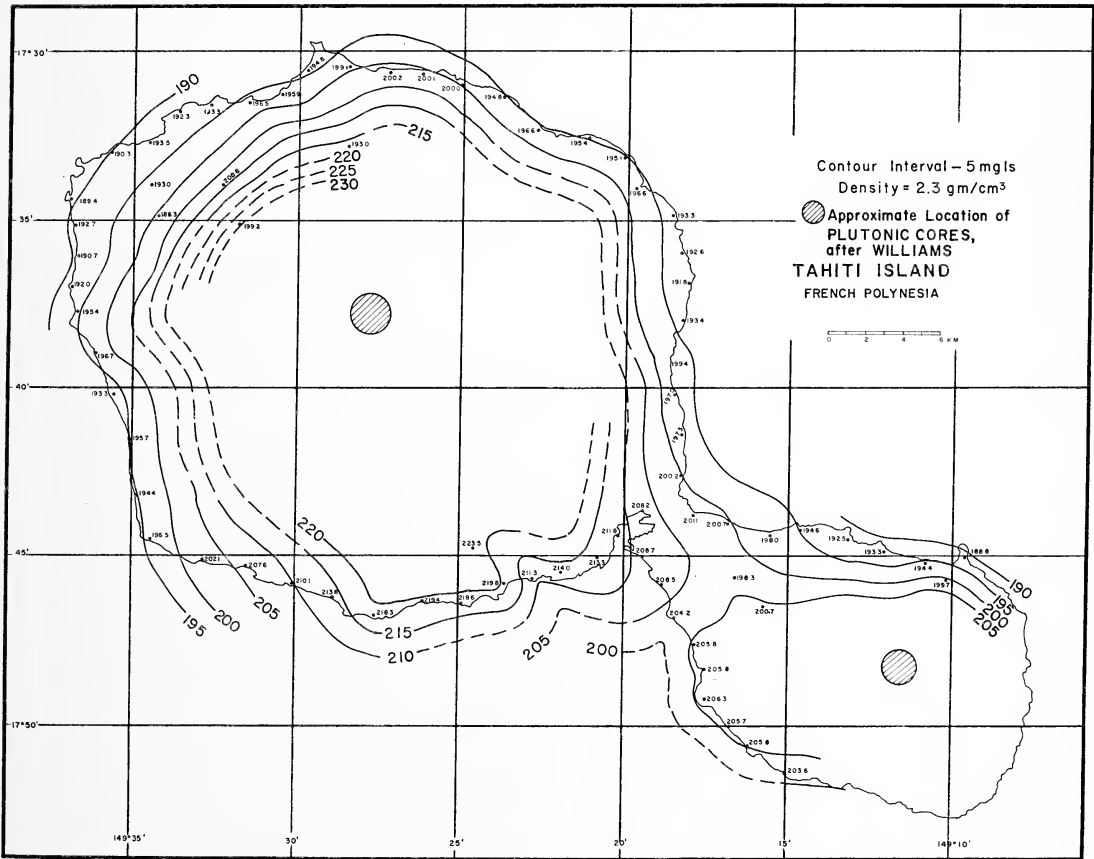


FIG. 4. Bouguer anomaly map of Tahiti I., French Polynesia.

mgal going southeast into the interior. Projecting from the coast the observed maximum gravity gradient of 20 mgal per mile would result in a +300-mgal maximum at the center. Only one high is apparent from the data. Numerous rift zones are discernible trending in the northeast, north, west, and southeast directions.

The Bouguer anomaly map of the Tairapu Peninsula (Fig. 4) shows contours elongated in an east-west direction separated from the Tahiti-Nui anomaly by the +205-mgal contour line. The lowest observed value was +189 and the highest was +205 mgal. The maximum gradient was 10 mgal per mile, occurring on the northeastern end of the peninsula. Projecting this to the southwest would give a maxi-

imum value of +230 mgal at the center of the caldera, with the gravimetric center closely coinciding with the given geologic position. Although the gravimetric data support the geologic locations of the caldera, they do not substantiate the observed changes in lithology. According to the gravity data Tahiti-Nui is more basic than is Tairapu Peninsula.

Moorea

Topographically Moorea is the complete opposite of Tahiti, appearing in profile as a series of jagged peaks separated by moderately sloping valleys. The island is triangular in shape, measuring 10 miles on each side; and the highest point, located south of the island center, is

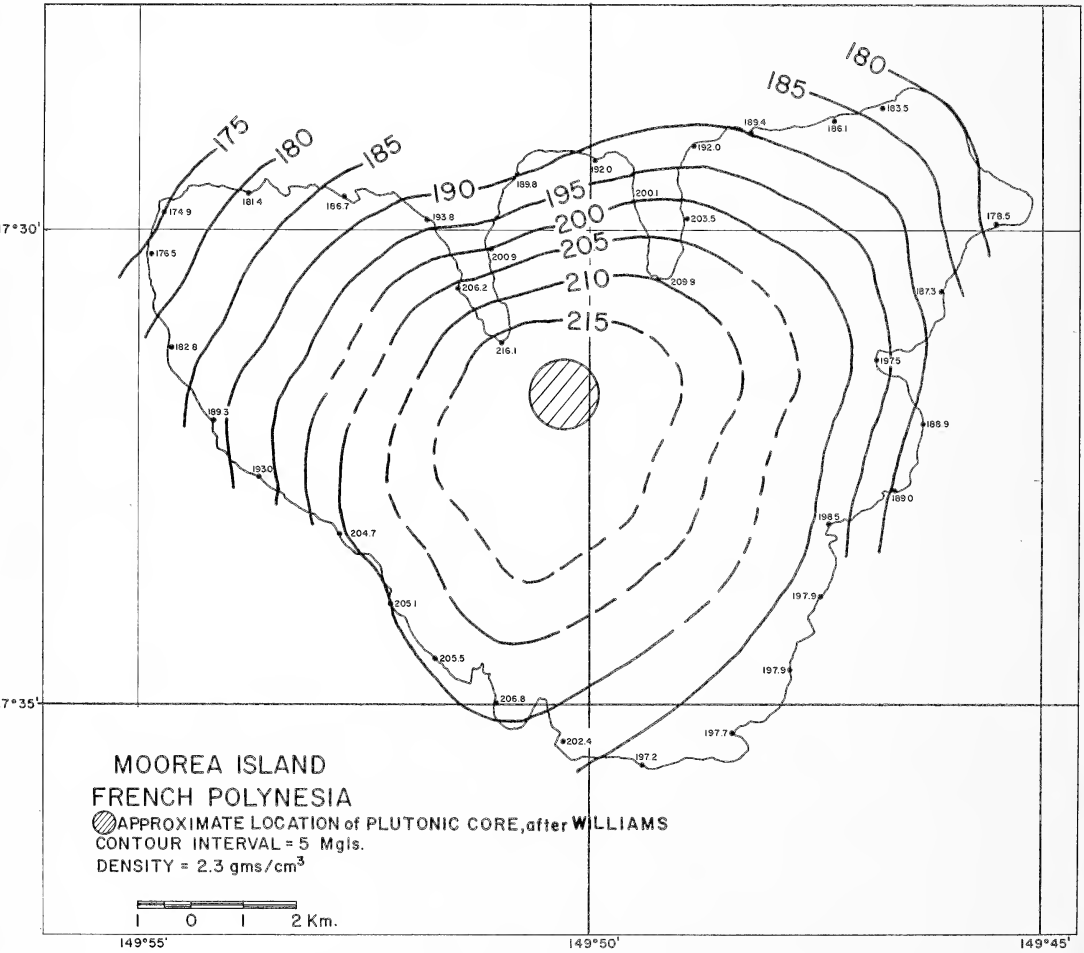


FIG. 5. Bouguer anomaly map of Moorea I., French Polynesia.

3975 ft. Fringing and barrier reefs surround the island. Geologically, Moorea differs from Tahiti in that there is an absence of visible intrusive rocks. The primary outcropping rock is a basaltic lava with subordinate amounts of nepheline-bearing trachytes and some andesites. The geologic position of the caldera has been fixed northeast of the center of the island. The entire area of the caldera is effectively covered by a mantle of laterite; consequently, the exact nature of the volcanic plug cannot be ascertained by surface examination.

The gravity contours (Fig. 5) form a roughly triangular shape corresponding to the shape of the island. The lowest value of +195 mgal was found in the northwest while the highest value of +216 was found near the assumed center of the caldera. The maximum gradients of 11 mgal per mile, outlining probable rift zones, occur trending north, northwest, and northeast from the gravity high with the minimum gradient trending southwards. Because of the absence of roads, an extensive series of observations into the center of the caldera area was impossible. Projecting the gravity gradient southward, however, would produce a +225-mgal Bouguer anomaly maximum over the caldera. The gravimetric center would then be in approximately the same position as the geologic center described by Williams (1933). Inasmuch as the absolute Bouguer gravity anomaly values are all similar to those observed in Hawaii, it is probable that the island platform is composed of tholeiitic basalt, but that the pipe material is basic rather than ultrabasic in character.

To summarize, the gravity field observed on Tahiti and Moorea conforms closely with the topography and geology of the islands. A steeper gravity anomaly gradient as the main caldera on Tahiti-Nui is approached suggests a value not unlike those observed in Hawaii (+300 mgal). Direct observations were precluded by the mountain jungle interior. On Moorea observations near the caldera area were possible. The gradient, however, was only +11 mgal per mile, and the maximum Bouguer

anomaly probably does not exceed +225 mgal. This value is only slightly higher than the mass effect to be expected for the island platform. The pipe effect, therefore, is quite small as compared with that observed in the Hawaiian Islands and as projected on Tahiti.

#### ACKNOWLEDGMENTS

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# Gravity and Magnetic Fields Over the Proposed Moho Hole Site North of Maui<sup>1</sup>

JOHN C. ROSE and JOHN C. BELSHÉ

DURING 1964 the Hawaii Institute of Geophysics carried out two marine surveys of the area north of Maui. These surveys provided the gravity, magnetic, and bathymetric data which will be discussed in this paper. The first survey was made by J. C. Rose on the Bureau of Commercial Fisheries ship "Charles H. Gilbert," using a LaCoste-Romberg shipboard gravimeter loaned by the University of California at Los Angeles. The second was conducted under a cooperative program with the U. S. Coast and Geodetic Survey on the hydrographic survey ship "Surveyor," under the command of Captain R. Jones with Mr. Kenneth Culler representing the Hawaii Institute of Geophysics. Position points along the tracks of these operations are shown in Figure 1.

Subsequently, there have been two magnetic measuring cruises on the Hawaii Institute of Geophysics vessel R/V "Teritu."

## PREVIOUS STUDIES

Many earlier studies have been made of the gravity and magnetic fields in the vicinity of the Hawaiian Islands. Most of the early work was confined to submarine gravity measurements, starting with the pioneer round-the-world trip of Vening Meinesz in 1925 and continued by the Lamont Geological Observatory in the years immediately following World War II. The operations made on the U. S. submarines "Capitaine," SS 336; "Sea Dog," SS 401; "Bugara," SS 331; and "Rock," SS 274 were by various observers, but mostly by Dr. J. L. Worzel. The subsequent surface ship operations involving both gravity and magnetic observations were made by the "Argo," operated by the Scripps Institution of Oceanography, which carried out local surveys during cruises Monsoon and Dodo while on her way to participate in the Interna-

tional Indian Ocean Expedition. One of the authors (Belshé) was aboard during both of these operations, and the other participated in the second. Measurements have also been made by the "Rehoboth" operated by the U. S. Navy Oceanographic Office, and by the "Surveyor" and the "Pioneer" operated by the U. S. Coast and Geodetic Survey. During the spring 1964 operation of the "Surveyor," Dr. P. Dehlinger of Oregon State University was in charge of the gravity program. The authors are indebted to all these groups for their cooperation in making available the information from these cruises.

Most, but not all, of the gravity information from these earlier studies has been used in the gravity analysis presented in the paper in this issue by Strange et al. (p. 381 in this issue). It can be seen from Figure 2 that detailed coverage in the area of immediate interest (centered on 155°28'W, 22°22'N) is not as good as one might wish, although probably adequate for present purposes—the determination of the gross field and any significant abnormalities in the crust or mantle in the general area of the proposed Moho Hole site.

## NARRATION OF THE "GILBERT" OPERATION

Arrangements were made in May 1964 between the Hawaii Institute of Geophysics, the Office of Naval Research, and the University of California at Los Angeles, for the loan of a LaCoste-Romberg sea gravimeter S3 for two weeks.

Through the cooperation of the Bureau of Commercial Fisheries, the ship "Charles H. Gilbert" was made available for the survey. The ship conducted underway gravity and bathymetric observations between 0445Z, May 30, and 1400Z, June 4, 1964. Position points for the ship's track during observations are shown on Figure 1. Because of the relatively small size of the ship and the prevailing sea and wind di-

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 98.

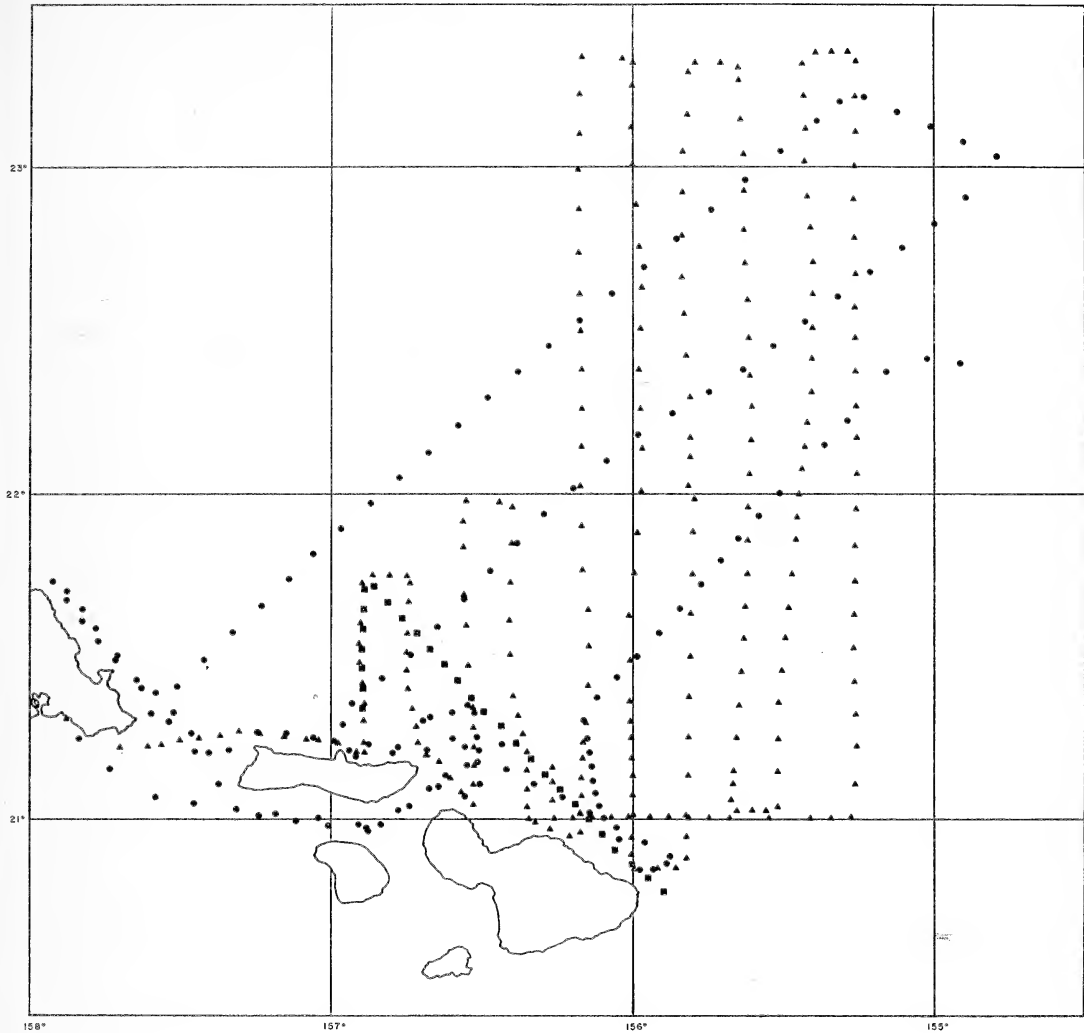


FIG. 1. Position points along the ship's tracks of R/V "Charles H. Gilbert" (*circles*) and of R/V "Surveyor" (*triangles and squares*).

rection, northeast-southwest tracks were chosen. This heading also resulted in the profile tracks being perpendicular to the structural strike of the Hawaiian Swell. Sea conditions were unusually calm during the entire cruise, allowing approximately 1000 miles of gravity observations out of approximately 1170 miles of total cruise. A note of unusual interest is that for the three crossings of the Molokai channel (usually characterized by confused high seas) the seas were abeam, yet the Browne correction was only 200 mgal on the last crossing and less than 100 mgal on the first two crossings.

The Browne corrections for the long southwest-northeast tracks were approximately 300, 200, and 400–600 mgal for the west, central, and eastern tracks, respectively. The central and eastern tracks had following seas. The tracks close to the islands generally had total Browne corrections of approximately 100 mgal. Bathymetry was obtained from the "Gilbert's" fathometer to 250 fm, and from E. L. Hamilton's 1953 and 1954 (unpublished) bottom contour charts northeast of Oahu, and F. P. Shepard's (unpublished) bottom contour charts of Kaneohe Bay and of the north coast

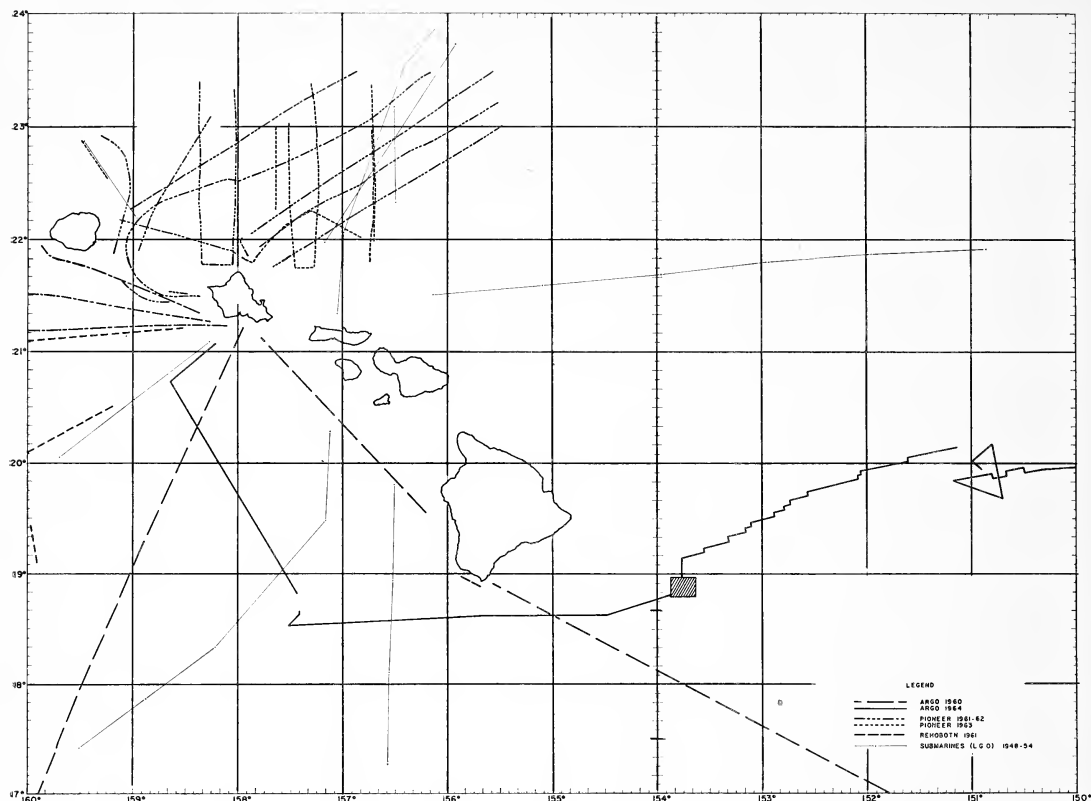


FIG. 2. Ship's tracks of gravity and magnetic studies in the Hawaiian Islands area performed by vessels other than R/V "Charles H. Gilbert" and R/V "Surveyor."

of Molokai. Additional information was obtained from the preliminary BC 1604 and BC 1605N charts of the U. S. Navy Oceanographic Office. Corrections were made for sound velocity in Hawaiian waters using a temperature vs. depth curve derived from data in Seckel (1955), McGary (1955), Seckel (1962), and Muromtsev (1963), and from the tables of sound speed in sea water (U. S. Naval Oceanographic Office, 1962).

The speeds used on any one straight track were weighted means, weighted according to the time interval between successive position fixes. Ship's position was determined from Loran C as well as radar and visual fixes.

Gravity results were computed on the University of Hawaii IBM 7040 computer, using an adapted program obtained from M. D. Helfer of the University of California at Los Angeles.

#### NARRATION OF THE "SURVEYOR" OPERATION

The "Surveyor" conducted underway gravity, magnetic, and bathymetric observation in the area north of Maui from 2110Z, September 28, to 2026Z, October 2, 1964. Position plots for the ship's track during this survey are shown on Figure 1. The tracks define a series of north-south lines spaced approximately 10 miles apart. Six long lines centered on  $155^{\circ}45' W$  give good coverage of the area 120 miles north of Maui, over the Hawaiian Arch, where Shor and Pollard (1964) report depths to the mantle of about 9 km. West of this area four shorter lines cover an area 20 miles north of Molokai and Maui, where Shor and Pollard (1964) report sub-Moho seismic velocities at depths of 5.8-7 km. This area is also characterized by a large positive magnetic anomaly (Malahoff and Woollard, in a forthcoming issue

of *Pacific Science*) centered over the island shelf at a depth of 500 m.

The gravity measurements were made with the LaCoste-Romberg sea gravimeter S12. Magnetic measurements were taken with a direct reading proton precession magnetometer, Varian model V4931DR. A narrow beam vertical sonar array produced by the Harris Company was used as the precision echo sounder for bathymetry. Navigation information relied heavily on Loran C for distant coverage and radar and visual observations when near the islands.

The ship's position was plotted every 15 minutes during most of the cruise (Figure 1). Data (time, depth, gravity, and magnetic force) were logged every minute. The depth information was read in fathoms from a precision graphic recorder. Its accuracy is  $\pm 1$  fm ( $\pm 1.83$  m). The time was recorded digitally on the minute from a crystal-controlled clock and should be accurate to  $\pm 3$  sec. The total force of the magnetic field was recorded to an accuracy of  $\pm 1$  gamma from a digital frequency meter.

The gravity measurements consisted of four record sets. The beam position of the heavily damped gravimeter was averaged over a  $3\frac{1}{2}$ -minute interval and presented digitally by a computer. The average beam position and the average meter counter setting were displayed graphically on a potentiometer recorder. Two pairs of galvanometer recorders displayed the short-period and long-period ham records, showing the nature of the horizontal accelerations affecting the instrument.

The digital data for time, magnetism, and gravity were recorded every minute, on the minute, by a Friden paper tape perforator in a B.C.D. form. This data tape could be printed out on a Flexowriter; an example is shown as Figure 3. The paper tape generated during the cruise was converted to a magnetic tape using the 1401 computer at the Statistical and Computing Center of the University of Hawaii, and the magnetic tape was then used directly in data processing with the IBM 7040 computer. Navigational control data, including the ship's heading and speed, and depth data were provided from a second magnetic tape which was

generated from punched cards prepared at the end of the cruise.

In the data processing program depths in fathoms were converted to meters and then corrected for sound velocity variations by an interpolation formula. The gravity value was an average value centered at 105 sec before it was recorded. The magnetic value represented a spatial point where the ship had been approximately 30 sec earlier than the time of recording. Therefore, both the recorded gravity and magnetic values were adjusted by simple averaging to correspond in real time to the depth record. The magnetic values were corrected for ship's heading and diurnal variation (using records from the magnetic observatory operated by the U. S. Coast and Geodetic Survey at Ewa Beach, Oahu). The observed gravity values were computed after the instrument variations were adjusted to the base value established by ties to the absolute gravity base site at Honolulu on September 21 and October 11. (The drift between these ties was 0.7 mgal.) The Eotvos correction term, using the ship's course and speed, was incorporated in the computation.

The computed values for depth, gravity, free-air gravity anomaly, and magnetic force were printed out by the computer in one-minute intervals. These values were also plotted graphically as profiles by a computer plotting program. Figure 4 is an example of such a plot for the

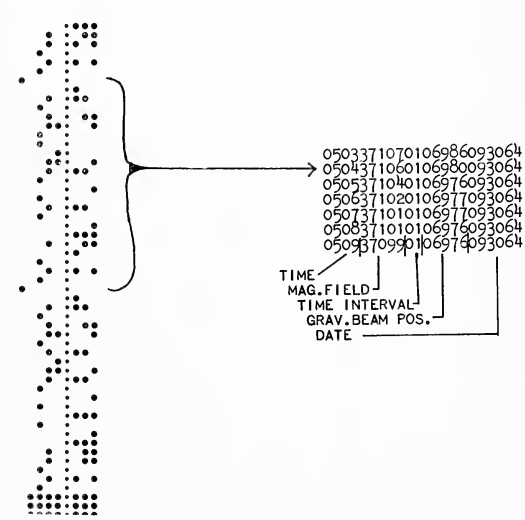


FIG. 3. Perforated paper data tape from R/V "Surveyor."



most westerly of the long north-south tracks. On these plots time is represented as a sequential minute number beginning at 2110Z, September 28. This particular plot follows 156°10' W, and extends from 20°56'N to 23°20'N. The depth record begins on the shelf north of Maui, shows the drop into the deep, and rises onto the Arch, where it terminates. Negative excursions on the free-air anomaly curve, as are seen at time numbers 1580 and 1730, represent erroneous readings caused by excessive acceleration corrections and are related to changes in ship speed.

DISCUSSION OF COMBINED RESULTS

In constructing the free-air anomaly contour map of the Moho Hole site area (Fig. 5),

gravity results for the "Surveyor" north-south track were arbitrarily adopted as control data for correction of the other data. The first step was to correct the cross-cutting "Gilbert" lines of measurements. These in turn were used to correct the south-north "Surveyor" tracks. The adoption of the quartering sea north-south tracks as a control is in accord with results reported by Dehlinger (in press). The corrections adopted were -9, +7, and -23 mgal for the west, central, and eastern "Gilbert" long lines, respectively, and +15 mgal for each of the three south-north "Surveyor" lines. No adjustments were made for the lines close to the islands, as the Browne corrections were generally 100 mgal or less.

It should be noted that the free-air anomaly

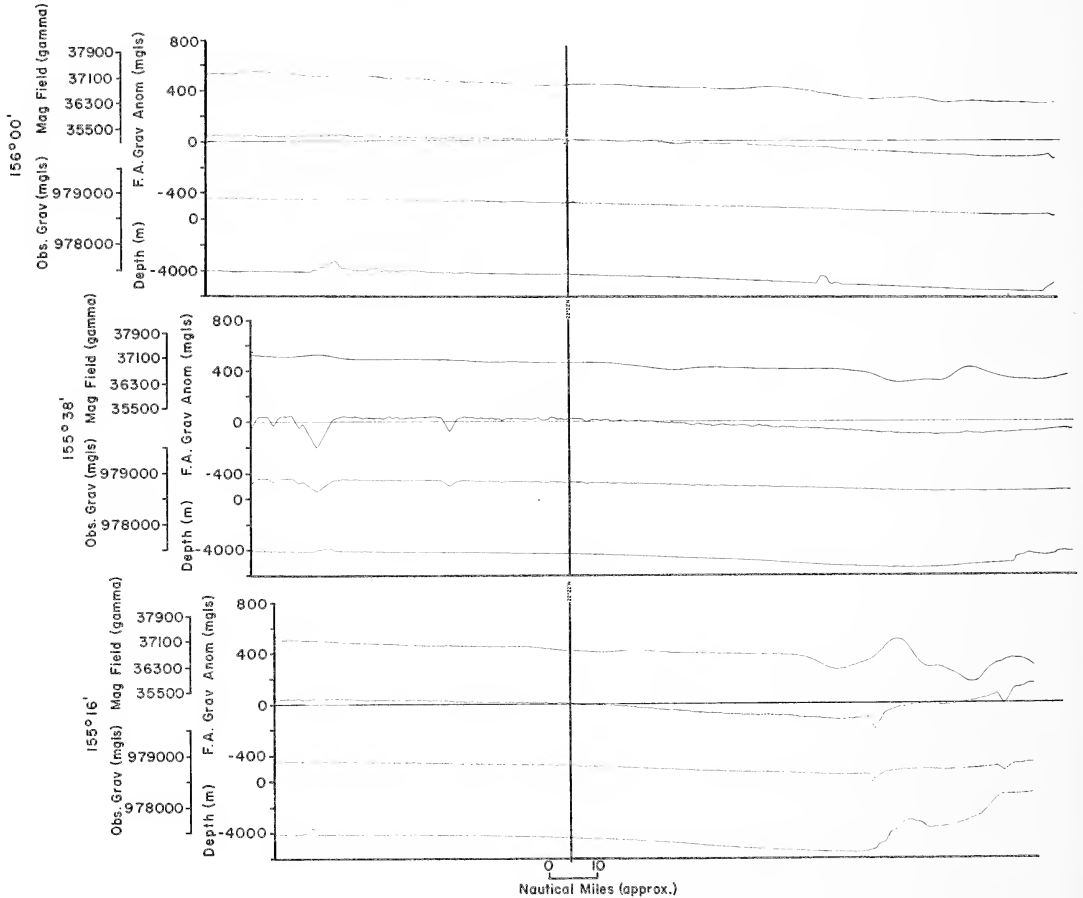


FIG. 4. Computer-plotted profiles of depth, observed gravity, free-air gravity anomaly, and magnetic force along a ship track of R/V "Surveyor."

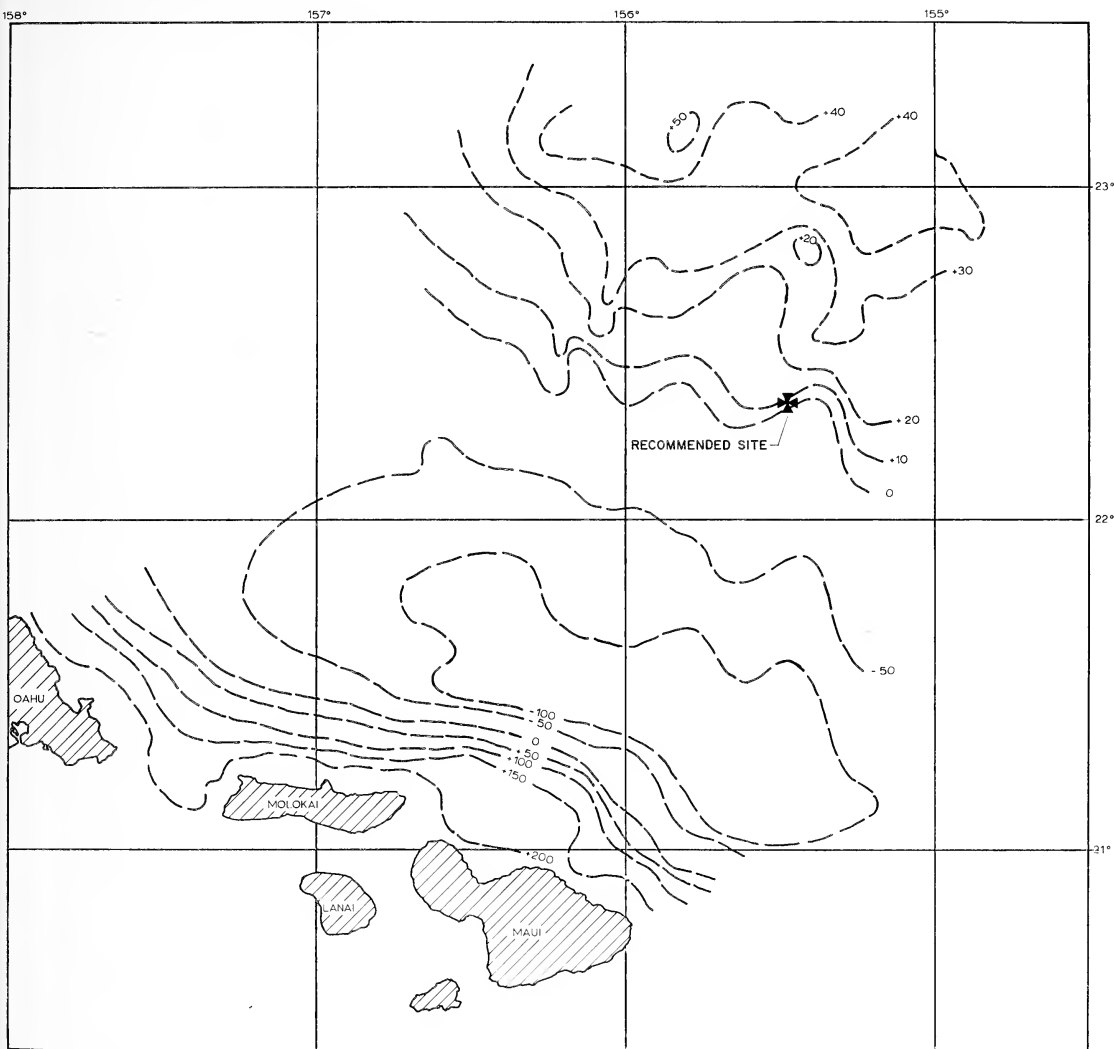


FIG. 5. Free-air anomaly map of the area north of Maui.

map (Fig. 5) differs slightly from the map by Strange et al. (Fig. 3, p. 386 in this issue), and reflects the effect of later detailed data that were not available at the time their map was drawn. The map of the total magnetic field north of Maui is given as Figure 2 in the paper by Woollard in this issue (see p. 282). Figure 4 shows three profiles made by the "Surveyor" as north-south runs. The proposed Moho Hole site lies midway between the profiles following 155°38'W and 155°00'W. The three profiles have been aligned at the point in time where they cross 22°22'N. As indicated

by Strange et al., and as shown here, the proposed Moho Hole site lies very near the point where the free-air anomaly changes from a positive field over the Arch to a negative field in the Hawaiian Deep. As the analysis of the earlier ("Gilbert") gravity data by Strange et al. is not materially affected by the additional ("Surveyor") data, these new data do not significantly alter the geological interpretation. The positive free-air anomaly near the proposed Moho Hole site can not be explained entirely by water-depth change and, as shown by Strange et al., can be recon-

ciled with the decrease in the depth to the Mohorovicic discontinuity.

Similarly, the more complete reduction of the magnetic data does not alter the gross picture presented by Malahoff and Woollard (in a forthcoming issue of *Pacific Science*) based on a preliminary reduction of the "Surveyor" data. As indicated by the depth analysis by Malahoff and Woollard, the depth of origin of the anomaly is somewhat greater (8.5 km) than the seismic depth to the Moho (5.8–7.0 km). The explanation for this discrepancy can be attributed to (a) the lack of precision in magnetic depth estimates, or (b) a difference in the depth at which there is a concentration of ferromagnetic minerals from gravity setting of heavy, early-formed minerals in an intrusion. Of the two explanations, the latter is considered the more probable in this case.

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# An Analysis of the Gravity Field Over the Hawaiian Islands in Terms of Crustal Structure<sup>1</sup>

WILLIAM E. STRANGE, GEORGE P. WOOLLARD, and JOHN C. ROSE

DURING THE PERIOD October 1963 to December 1964, some 750 gravity stations were established by the Hawaii Institute of Geophysics on islands of the Hawaiian Chain. About 600 stations were established on the major islands of Oahu, Molokai, Lanai, Kahoolawe, and Maui, and about 136 others on many of the smaller islands and islets from Nihoa to Midway. In addition, more than 500 stations have been established by personnel of the U. S. Geological Survey on the islands of Hawaii, Molokai, Maui, Lanai, Kauai, and Niihau. These results are presented in detail elsewhere in this issue. A number of shipboard gravity surveys, which are also reported in greater detail elsewhere in this issue (Rose and Belshé, p. 374) have produced a large amount of gravity data from the ocean areas surrounding the major islands at the southeast end of the Hawaiian Ridge. By using the shipboard data in conjunction with the land data, a composite anomaly map of a portion of the Hawaiian Ridge between Oahu and Maui was prepared and is presented in Figure 1.

This wealth of new gravity data, combined with the large increase in other forms of geologic and geophysical knowledge concerning the Hawaiian area, now makes possible a meaningful interpretation of the gravity data in terms of the gross structure of the Hawaiian Swell. We present in this paper a picture of the structure of the Hawaiian Swell which, it is believed, not only fits the observed gravity field but also is compatible with all other available geologic and geophysical information.

## SUMMARY ON DENSITY INFORMATION

As is well known, it is usually possible in interpreting gravity data to construct a number

of different mass distribution models, all of which can equally well account for the observed gravity field. A meaningful gravity interpretation must define a model which not only will satisfy the observed gravity field, but will also be compatible with known densities and available geologic and seismic information on structural variations at depth. Therefore, before describing the mass distribution model used to explain the observed gravity field of the Hawaiian Islands, the data which were considered in establishing the density values will be discussed.

Direct measurements of densities of rock of the Hawaiian Islands began with the work of Washington (1917), which was summarized by Woollard (1951). Goranson (1928) quoted a measurement by E. S. Shepherd on a typical block of pahoehoe having a density of 2.0 g/cc. Kinoshita et al. (1963) report that the dry density of 63 samples from the denser part of flows on the island of Hawaii ranged from 1.8 to 3.0 g/cc and averaged 2.3 g/cc. Measurements on flows for the island of Oahu carried out at the Hawaii Institute of Geophysics gave dry densities varying between 2.3 and 2.9 g/cc. Some dense olivine basalts from the island of Hawaii have densities lying between 2.8 and 3.1 g/cc. An amphibolite from the Koolau caldera on Oahu gave a density of 3.0 g/cc, while a weathered eclogite had a density of 2.8 g/cc. Manghnani and Woollard (p. 291 in this issue) found that most of the cores from the solidifying materials on the lava lake in Alae Crater, Hawaii, have densities of 2.5–2.8 g/cc. James Moore (unpublished) of the U. S. Geological Survey sampled lavas along the rift zones off the coast of the island of Hawaii. He found that the vesicle space and the size of vesicles decreased with water depth until at about 1.0 km below sea level there were essentially no vesicles. The change in density noted was from 2.2 g/cc at

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 99.

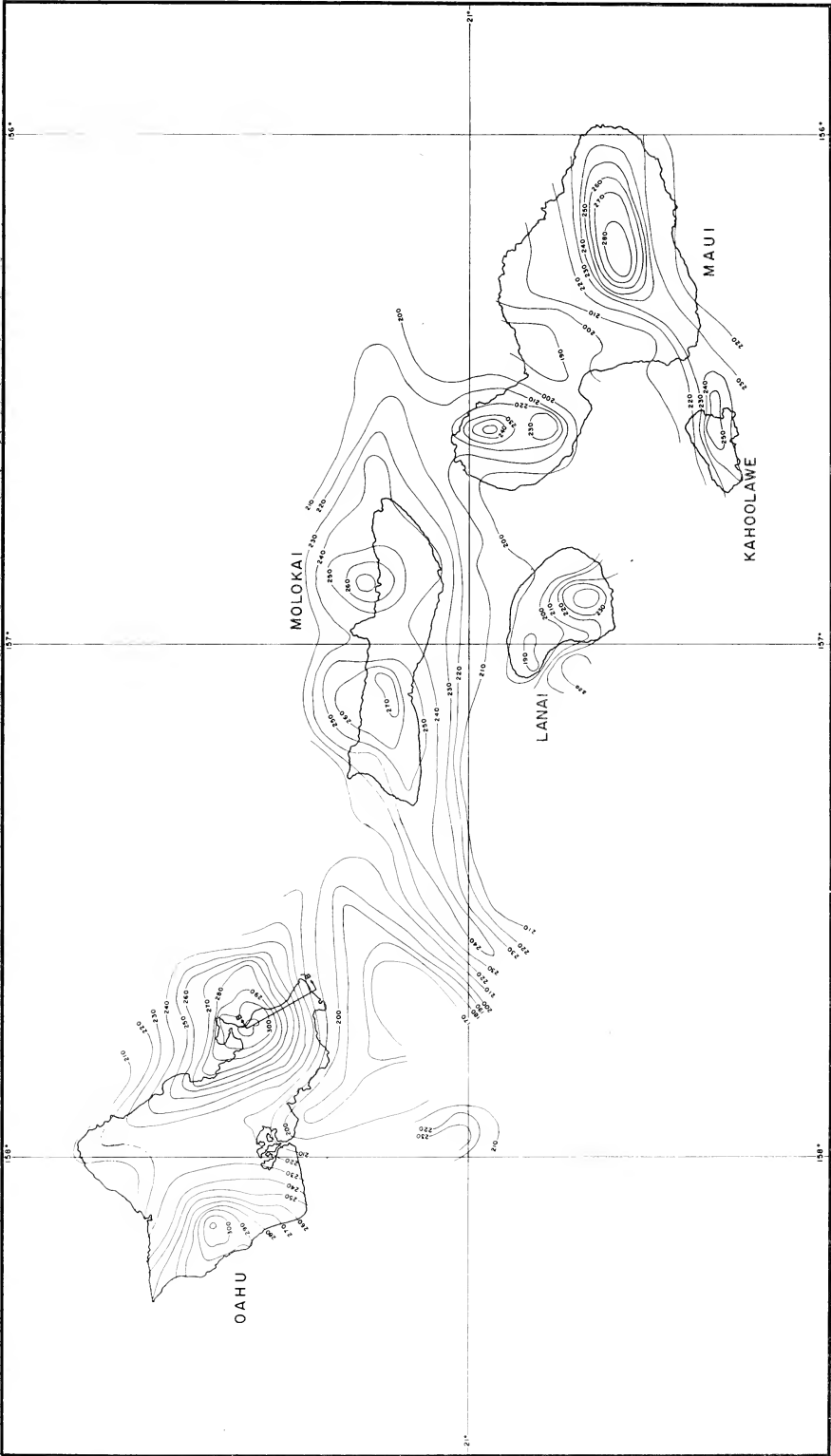


FIG. 1. Bouguer anomaly map of a section of the Hawaiian Ridge;  $\rho = 2.3 \text{ g/cc}$ . Contour intervals are at 10 mgal.

the surface to 2.9 g/cc at 1 km below sea level. At greater water depths the densities reached a maximum of about 3.0 g/cc.

It should be noted that all the density measurements described above are on small samples and thus give only the density of the individual rock samples. In addition there are negative contributions to the bulk density of the island masses by the vugular-type porosity associated with lava tubes and intraflow voids. It should also be noted that the densities given are dry densities. On the basis of the densities of non-vesicular samples, the grain densities of Hawaiian rocks should range upward from 2.9 g/cc to more than 3.0 g/cc, depending upon the percentage of olivine present. If we adopt a reasonable whole rock grain density of 3.0 g/cc, we can, if we assume perfect permeability, compute the relation between dry density and wet density as a function of porosity. The assumption of perfect permeability is justified, as it is known from ground-water studies that water table coincides closely with sea level in the Hawaiian Islands and is essentially independent of surface elevation. The volcanic flow material both above and immediately below sea level therefore appears to be not only porous but quite permeable. Under these conditions dry density values should be approached above sea level and wet density values below sea level, where the majority of the vesicles are filled with water. On the basis of the derived relation between dry and wet density values to be expected (Fig. 2), there should be a discontinuous density change of between 0.2 and 0.3 g/cc at sea level. This factor, which has been generally overlooked in past analyses of the gravity field

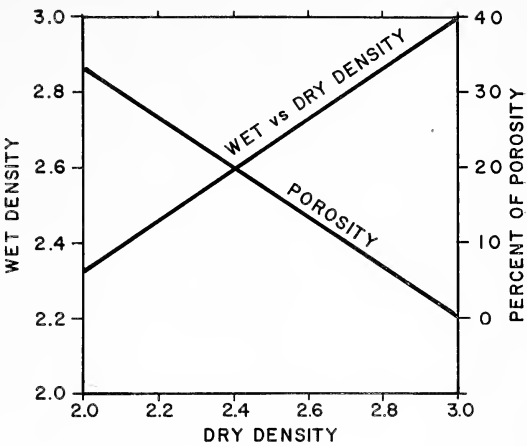


FIG. 2. The relation of water-saturated density and dry density basalt as a function of porosity.

of the Hawaiian Ridge, places some important restraints on the density distribution which can be assumed. If the bulk density of the island mass were 2.3 g/cc below sea level, as derived by Woollard (1951), then the mean density above sea level must be only about 2.0 g/cc, and this is the density which should be used to reduce land gravity observations to sea level. On the other hand, if the mean dry density above sea level is 2.3 g/cc, as determined by Kinoshita et al. (1963), then below sea level the density should be about 2.55 g/cc. One can test the probable density above sea level by comparing the relation between elevation and the Bouguer gravity anomalies in an area of broadly varying changes in surface elevation. Table 1 shows the effect on the maximum Bouguer anomalies for the island of Ha-

TABLE 1  
RELATION OF BOUGUER ANOMALIES TO VOLCANIC PEAK ELEVATIONS ON  
THE ISLAND OF HAWAII AS A FUNCTION OF DENSITY

PEAK	ELEVATION (ft)	BOUGUER ANOMALY		DIFFERENCE (mgal)
		$\sigma = 2.3 \text{ g/cc}$ (mgal)	$\sigma = 2.0 \text{ g/cc}$ (mgal)	
Mauna Loa.....	13490	+305	+370	+65
Mauna Kea.....	12380	+301	+360	+59
Kohala.....	4026	+305	+324	+19
Kilauea.....	3642	+313	+330	+17

waii if a density of 2.0 g/cc were assumed for the material above sea level, rather than a density of 2.3 g/cc. As can be seen, the effect of reducing the density is to raise the anomaly values and to give a positive correlation with surface elevation. A density of 2.3 g/cc, therefore, appears to be more correct, as it yields anomalies which show no correlation with local changes in surface elevation.

The densities of the materials in the sub-surface cannot be sampled directly but must be established indirectly. One of the best sources of indirect evidence as to the densities present is seismic information. In addition to the seismic work carried out on the Hawaiian Ridge by the Hawaii Institute of Geophysics and reported by Furumoto et al. (p. 306 in this issue) and Adams and Furumoto (p. 296 in this issue), explosion seismic refraction measurements have been made in the waters adjacent to the Hawaiian Islands by Raitt (1956), Gaskell and Swallow (1953), Shor (1960), Shor and Pollard (1964), and Western Geophysical Company (unpublished). In addition, Jones (1935) and Eaton (1962) have used observatory earthquake information to study the velocity structure on the Hawaiian Ridge. Although details vary, the seismic results present an amazingly consistent picture of the over-all velocity structure of the Hawaiian Ridge and the area around it.

Over the shallow waters on the Ridge and on the islands away from volcanic pipes and rift zones, the velocity structure consists of 2-3 km of material with a velocity lying between 2.9 and 4.0 km/sec, 6-8 km of material with a velocity between 4.5 and 5.2 km/sec, and 4-7 km of material with a velocity between 6.4 and 7.2 km/sec, with the depth to Moho ranging from 14 to 16 km. The only significant deviation from this picture is seen in the results obtained by Furumoto et al. (see p. 306 in this issue), which show a much thicker lower crustal layer and a Moho depth of 20+ km. However, this depth does not appear to be representative of the Ridge as a whole, which appears to be 14-16 km. This does not imply that the 20-km depth south of Oahu is incorrect, for, as is seen in the gravity map of Figure 1, a thicker crust there is substantiated by a

pronounced gravity minimum over the area that cannot be related to bathymetry or to a thick section of sediments.

A drastically different picture is found from seismic work carried out over the volcanic plugs or along major rift zones. Here velocities in excess of 7.0 km/sec—usually in the range of 7.5-8.0 km/sec—are found at depths from 2 to 7 km below sea level. This material is sometimes overlain by material whose velocity is about 6.0 km/sec. Examples of this can be seen in the papers by Furumoto et al. and Adams and Furumoto in this issue. These results are similar to those obtained elsewhere in the Hawaiian area by other investigators.

In the case of Hawaiian volcanic rocks, special care must be taken in converting velocity information to density information since the relations which exist are considerably different from those commonly encountered in continental-type igneous rocks. These differences result primarily from three factors: (1) the exceptionally high grain density of the Hawaiian rocks, (2) the very large porosities which exist, and (3) the presence of glass.

Manghnani and Woollard (p. 291 in this issue) summarize laboratory velocity measurements of a number of Hawaiian rocks at surface temperatures and pressures. They find that the velocity of the basalts is controlled by the amount of glass and olivine present as well as by the physical structure of the rock. When using these laboratory measurements to relate seismic velocities observed in the field densities, it is important to correct for changes in environmental conditions. In addition to the effect of the difference in ambient temperature and pressure, there is also the effect of interstitial water pressure on the very porous lavas. The effect of interstitial water pressure, however, is closely related to permeability, and these workers have found a definite correlation between seismic velocity in flow material and apparent porosity which appears to be related to differences in permeability.

In clastic sediments, the hydrostatic pressure of the water in the pore spaces has been shown by various investigators to result in a decrease in velocity with increasing pore water pressure. This effect in sediments apparently results from

the fact that water, being incompressible, supports a part of the overlying rock load, and thus the rock particles are not in as solid a contact as they might be if the water pressure were not present. In lavas the material is not made up of individual particles, but if fine cracks were present they might serve effectively to break the material up into individual particles. The effect of both the presence of glass and the interstitial water pressure is to cause a lower velocity for a given density than one might otherwise expect. Both of these factors, therefore, probably influence the density-velocity correlation associated with lavas in a marine environment.

The interstitial water could have another effect also: It could help to explain the apparent retention of rather high porosities to great water depths. The effective pressure on the solid rock material at any depth would be  $(\sigma_r - \sigma_w)h$  rather than  $\sigma_r h$ , where  $\sigma_r$  is rock density,  $\sigma_w$  is water density, and  $h$  equals the thickness of overlying rock. Consider a point near the ocean floor, say 4 km below sea level, and material with a primary density of 2.3 g/cc. The difference in pressure under different assumptions would be:

For a density of 2.3 g/cc and no interstitial water:

$$P_1 = \sigma_r h = 2.3 \text{ g/cc} \times 4 \times 10^5 \text{ cm} = 9.2 \times 10^5 \text{ g/cm}^2$$

For a density of 2.3 g/cc with interstitial water:

$$P_2 = (\sigma_r - \sigma_w)h = 1.27 \text{ g/cc} \times 4 \times 10^5 = 5.08 \times 10^5 \text{ g/cm}^2$$

Or, if the rock is solid and  $\sigma_r = 2.9 \text{ g/cc}$ :

$$P_3 = \sigma_r h = 2.9 \times 4 \times 10^5 = 11.6 \times 10^5 \text{ g/cm}^2$$

The effect of pore water, therefore, would be to decrease appreciably the strength necessary to support the overlying material. Another factor which could produce porosity in the volcanic pile below sea level, and thus lower both the velocity and density, would be the presence of void spaces between successive flows of pillow lava.

#### CONSTRUCTION OF A DENSITY MODEL FOR THE HAWAIIAN SWELL

The most recent of previous interpretations

of the gross gravity field of the Hawaiian Islands in terms of density models are those of Woollard (1954), Talwani et al. (1959), and Worzel and Harrison (1963). In the light of present knowledge none of these interpretations is tenable any longer. The interpretation of Talwani et al. does not take into account the velocity structure of the Ridge, and assumes that materials with velocities which range from 4.0 to 7.0 km/sec have a density of 2.84 g/cc. Moreover, this interpretation would make it impossible to explain the local anomalies associated with the volcanic pipes without assuming an unreasonably high density for the material in the pipes.

The density model proposed by Woollard (1954), while reasonable at the time, must be rejected now on two bases. First, the boundary proposed in this model between the 2.3 and 2.9 g/cc layers would lie in the middle of the 5.0 km/sec seismic layer, and it is difficult to imagine a density change of 0.6 gm/cc without an attendant velocity change. Second, as pointed out earlier, in order to maintain a density of 2.3 g/cc to the level of seabottom requires either that the dry density of the material be about 2.0 g/cc or that the material be nearly impermeable so that the voids are not water-filled. Neither of these conditions seems geologically probable.

Taking into account all the information indicated in the previous section, a model representing crustal structure and composition across the Swell was constructed and the two-dimensional gravity program of Talwani et al. (1959) was used to compute the gravitational effect of the model. Figure 3 is the free-air gravity anomaly map of the Hawaiian Islands. Figure 4 presents the mass distribution model and a comparison of the observed and computed free-air gravity anomaly profiles along line A-A' of Figure 3. As seen, there is a reasonably good fit between observed and computed values.

The densities of 2.95 g/cc and 3.40 g/cc for the main oceanic crustal layer and the mantle respectively were chosen on the basis of the density velocity studies summarized in Woollard (1962). The density of 2.6 g/cc for the upper layer of the oceanic crust was chosen on the assumption that this layer represents a com-



bination of flow material and sediments with some porosity remaining. This picture more or less conforms to the results obtained in the preliminary Mohole drilling off the west coast of the United States.

The density of the sediments in the bathymetric deep adjacent to the Ridge was assumed to be 2.1 g/cc. This is in the range of densities normally chosen for such sediments, but admittedly it may be too low since it implies porosities in the neighborhood of 40 per cent throughout the sediments. The thickness of the sediments was chosen to match the seismic reflection results of Kroenke (p. 335 in this issue). On the Ridge itself the unsaturated density above sea level for the flows was assumed to be 2.3 g/cc. Below sea level, the porous rocks were assumed to be water-saturated and a density of 2.5 g/cc was used for the first 1.5 km below sea level. A density of 2.6 g/cc was then used for the next 1.5 km. Together these density

layers were chosen to represent material which had erupted above or near sea level.

The density of 2.75 g/cc was chosen for the bulk of the Hawaiian Ridge which has a seismic velocity near 5.0 km/sec, under the assumption that the low seismic velocity results primarily from the presence of glass but that some intraflow porosity between pillow lava flows exists. It might be mentioned here that a velocity of about 5.0 km/sec is a usual velocity for submarine volcanic flows and has been found in many other areas, such as along the Mid-Atlantic Ridge and on the Tonga Ridge.

The question might well be asked, what other density distributions are possible? Basically the geologically acceptable possibilities involve changing the densities by about  $\pm 0.1$  g/cc in all or part of any layer, with attendant changes in densities of other layers or slight meometric changes of  $\pm 1$  km in boundaries between layers. There is probably no way short

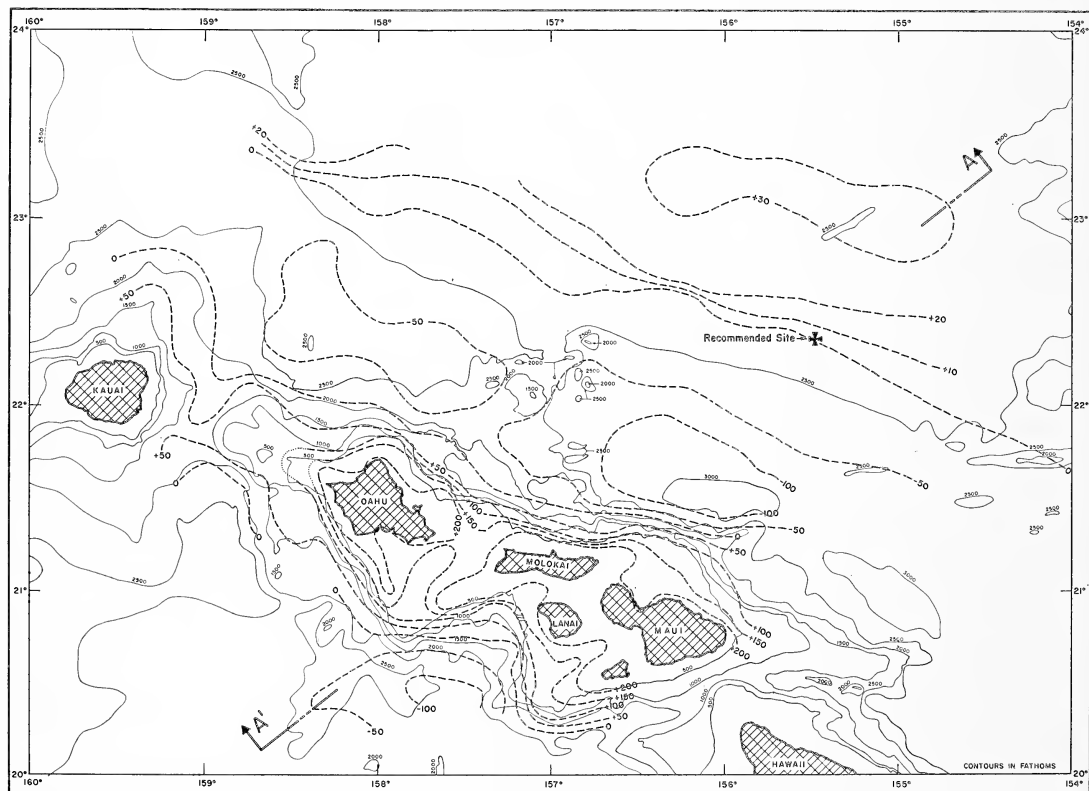
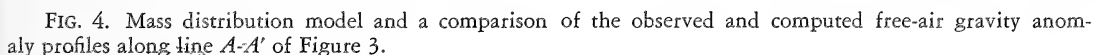


FIG. 3. Free air anomaly (dashed lines) gravity map of the Hawaiian Islands (values in milligals). Bathymetry contours (solid lines) in fathoms.



bodies. Despite this rather impressive array of restrictions, much latitude still remains as to choice of density model. As the Koolau volcanic center and rift zone have been more extensively studied gravimetrically and seismically than most of the other intrusive complexes, these features were chosen for the analysis. In addition, the gravity anomaly associated with the Koolau volcanic center is one of the larger anomalies and the center lies essentially at sea level. There are, therefore, fewer uncertainties in the gravity anomaly picture and more restraints on the mass distribution model constructed to represent this intrusive complex than on any of the other intrusive complexes. Thus, several models which would satisfy all of the known parameters associated with the Koolau volcanic center and

In constructing density models to represent the volcanic centers and rift zones, the primary constraints are: (a) the magnitude of the anomaly, (b) the shape of the anomaly, (c) the densities already chosen for the bulk of the Ridge with which the densities of the volcanic pipes and rift zones are to be contrasted, (d) the range of geologically permissible densities for the intrusive material, and (e) the seismic evidence as to dimensions of the intrusive

rift zone were studied. Rough calculations showed that, by assuming somewhat different geometric shapes and depths of burial and making slight changes in densities of less than 0.1 g/cc, density models which would have the same basic structure as those derived seismically for the Koolau caldera could be constructed that would satisfy the gravity field of the other intrusive complexes. The final model chosen to represent the volcanic pipe associated with the Koolau caldera is illustrated in Figure 5. This cross-sectional view implies a symmetrical model made up of cylinders or vertical prisms. Actually, the model used was not quite symmetrical. The model consisted of a number of vertical prisms  $0.5 \times 0.5$  km in horizontal dimensions, with the gravity effect of each prism computed assuming that its mass was concentrated along a line element at its center. The cross-sectional shape of the volcanic pipe was chosen to conform in its upper parts to geologic knowledge of the dimensions of the caldera and to the seismic information. Because of the complications due to the gravitational effects of the rift zones to the north and east,

this model is chosen essentially to fit gravity profiles taken from the center of the caldera in a western or southern direction and corresponds to the line of seismic measurements reported by Adams and Furumoto (p. 296 in this issue). As indicated, it assumes the same densities external to the pipe as those assumed for the Ridge as a whole and illustrated in Figure 4.

#### INTERPRETATION OF RESULTS

The composite section across the Hawaiian Swell based on seismic and gravity evidence is shown in Figure 4. This section seems compatible with most of the available evidence on the Hawaiian Ridge as well as on other oceanic areas.

As indicated by the gravity map in Figure 1, and as shown even more convincingly by the magnetic work of Malahoff and Woollard (in a forthcoming issue of *Pacific Science*), the lavas which built the Hawaiian Islands were extruded primarily along faults oriented either east-west and associated with the Molokai fracture system or northwest-southeast and associated with the trend along which lie the Koolau dike complex and the Musician Seamounts. The volcanic pipes may have formed at points of intersection of rifts of the two fracture systems. After an appreciable build-up of extrusive material, the weight of the extruded lavas caused the ridge to sink in order to re-establish isostatic equilibrium. Since the depth to Moho is about 15 km on the Ridge and about 11 km in the normal ocean basin, a thickening of the crust of some 4 km is indicated. Whether or not this also represents the degree of crustal subsidence is not definite as yet. The material with velocities in the range 2.5–4.0 km/sec and assumed densities of less than 2.6 g/cc is from 2 to 3 km thick and, judging from the work of Moore (unpublished), must have been erupted above or near sea level. These data, therefore, suggest roughly 2–3 km of subsidence. How much subsidence occurred prior to the build-up of the Ridge to sea level can only be surmised. It does appear significant, though, that the upper face of the basal crustal layer also indicates only 2–3 km of subsidence.

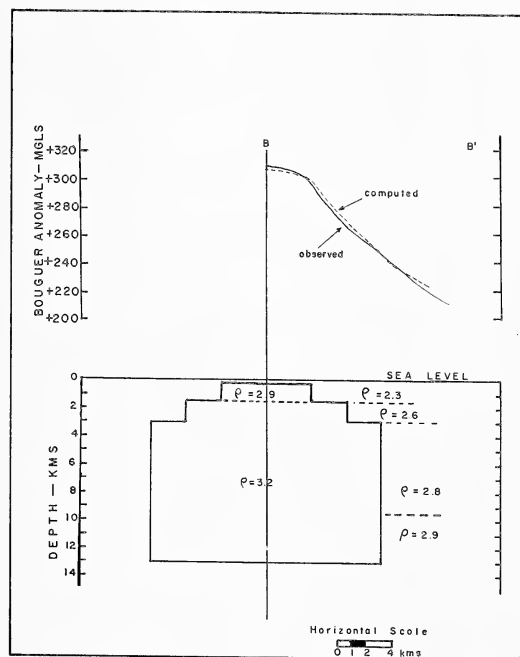


FIG. 5. Density model for the Koolau volcano, along line B-B' of Figure 1.

It is interesting to note the large cross-sectional dimensions which must be chosen for the volcanic pipes and rift zones at depth in order to explain the observed gravity anomalies. On the basis of seismic activity and tilt data Eaton (1962) has postulated that the magma which is erupting today on the island of Hawaii originates at some 60 km below sea level and rises through a conduit to a magma chamber a few kilometers below the surface, where it remains until sufficient force is built up to cause an eruption. He was able also to show that the lava migrated laterally from the magma chamber beneath the central pipe to erupt along the rift zone. From this one might postulate that the rift zones are rather surficial features formed when the central throat of the eruptive center became clogged with solidified material. However, the gravity data indicate that the rift zones are of two distinctly different types. Rift zones such as those in Haleakala crater on Maui have little gravity or magnetic effect and apparently are rather superficial features. However, rift zones with a large gravitational effect, such as the northwest rift zone of the Koolau volcanic center, are very basic structural features extending downward at least to the Mohorovicic discontinuity. Such an interpretation is also substantiated by the magnetic results obtained by Malahoff and Woollard (referenced above).

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# The Paleomagnetic Significance of Aeromagnetic Surveys of the Hawaiian Islands<sup>1</sup>

ALEXANDER MALAHOFF and WILLIAM E. STRANGE

**ABSTRACT:** Aeromagnetic surveys of the Hawaiian Islands have revealed that the primary magnetic anomalies associated with the islands are dipole anomalies caused by the intrusive rocks of the volcanic centers and rift zones. Comparisons of the direction of magnetization indicated by the dipole anomalies with results of laboratory measurements on lavas show that in many cases the lavas possess reverse polarization while the intrusive rocks are normally polarized. These results must be taken into account when interpreting the magnetic field of submerged marine volcanic features such as seamounts and when establishing periods of reversal in the earth's magnetic field.

AN AEROMAGNETIC SURVEY covering the major islands at the southern end of the Hawaiian chain has recently been completed with flight lines approximately 1 mile apart. The structural and geologic implications of this survey are discussed in detail by Malahoff and Woollard (in a forthcoming issue of *Pacific Science*), to which paper the reader is referred for examination of the actual anomaly contour maps. The dominant magnetic anomalies observed over the islands were found to be positive-negative anomaly pairs—typical dipole anomalies. Such anomalies might be expected to result from bodies with near vertical sides magnetized parallel to the present earth's field, which, in this area, has an inclination of 30–40°. From a comparison of the location of the dipole anomalies with the geologic and gravimetric data on the islands, it is apparent that they are caused by the intrusive rocks associated with the volcanic centers and major rift zones on the islands. Such a result is in agreement with laboratory determinations of susceptibility and intensity of remnant magnetization of some Hawaiian rocks made by the authors. These measurements show that the intensity of remnant magnetization is much greater in most intrusive rocks of the Hawaiian Islands than in the lavas. In both types of rocks the intensity of remnant magnetization greatly exceeded that of induced

magnetization—by a factor of 1:10 in olivine-poor samples. Several model computations showed that it is possible to explain the observed aeromagnetic anomalies by assuming that the intrusive rocks were either normally or inversely polarized in a direction nearly parallel to the present earth's field. This is in agreement with measurements by Tarling (1963) of direction of remnant magnetization carried out on surface samples, primarily lavas, which also indicated directions of remnant magnetization nearly parallel to the present earth's field. Because the magnetic anomalies caused by the remnant magnetization of the intrusive rocks are dipole anomalies, it is possible to determine by inspection whether the intrusive rocks are normally or inversely polarized. This gross direction of remnant magnetization (normal or reverse) is given in Table 1, along with the results obtained by McDougall and Tarling (1963), and Doell and Cox (1963), and measurements made by the writers on surface samples of both extrusive and intrusive rocks.

The paleomagnetic and age dating results obtained by McDougall and Tarling (1963) from Hawaiian lavas have been utilized by Cox, Doell, and Dalrymple (1964) in conjunction with data from other areas to establish alternating periods of normality and reversal in the earth's magnetic field during the last four million years. The reality of these reversals, their length (if they exist), and the

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 100.

TABLE 1  
SUMMARY OF GEOMAGNETIC RESULTS

FORMATION	POLARITY 1 <sup>1</sup>	POLARITY 2 <sup>2</sup>	POLARITY 3 <sup>3</sup>	POLARITY 4 <sup>4</sup>	K-AR AGE <sup>1</sup> M.Y.
Hawaii (historic)		N <sup>5</sup>	N	N	historic
Hana (East Maui)	N		N	} N	0.4
Kula (East Maui)	N		N		0.86, 0.43
Honomanu (East Maui)	R <sup>6</sup>		N		0.86
Honolua dike rocks			R	} R	
Honolua (West Maui)	R		R		1.15 ±0.02
Wailuku dike rocks			N		
Wailuku (West Maui)	R		R		1.29 ±0.03
Kahoolawe				N	
Lanai	R			N	
East Molokai	R			N	1.3-1.5
West Molokai	R			N	1.85 ±0.01
Koolau dike rocks (East Oahu)			N	} R	
Koolau (East Oahu)	R		N and R		2.2-2.5
	{ N N R N				2.76 ±0.02
				} N	2.84 ±0.02
Waianae (West Oahu)					2.95 ±0.06
					3.27 ±0.04
Koloa (Kauai)	N and R		N and R	N	
Napali (Kauai)	N		N	N	4.5-5.6
Niihau				N	

<sup>1</sup> As determined by McDougall and Tarling (1963) primarily from extrusive material.  
<sup>2</sup> As determined by Doell and Cox (1963).  
<sup>3</sup> As determined by present authors on rock samples, using an astatic magnetometer.  
<sup>4</sup> As determined by total magnetic intensity maps (intrusive rocks only).  
<sup>5</sup> Normal polarization.  
<sup>6</sup> Reversed polarization.

period of time over which the change from one polarity to the other took place, are extremely important in establishing a model for the main magnetic field of the earth. It is important, therefore, to explain the differences shown in Table 1 between the direction of magnetization of the bulk of the intrusive material, as revealed by the aeromagnetic survey, and that of the surface samples of the lavas. A number of possible explanations exist. The age of the bulk of the intrusive material usually is unknown and lavas of both normal and reverse polarization but different ages are sometimes found to be associated with the same volcanic center. The most obvious explanation for this difference would be that, for many centers of eruption, the bulk of the intrusive material solidified at a different time than did the lavas, whose directions of magnetization are different from the directions of magnetism of the in-

trusive material. At the present time it is not possible to confirm or disprove this or any other explanation for the differences. Detailed measurements of the ages and directions of remnant magnetization of the intrusive rocks of islands and determination of the types of magnetic minerals present are first necessary. It is worth pointing out, however, that differences between the direction of polarization of intrusives and extrusives which are almost certainly not due to age differences have been noted previously.

The aeromagnetic survey results also bring out several important facts which affect the interpretation of airborne or seaborne magnetic surveys over seamounts, guyots, and similar oceanic volcanic features. It has been common practice to assume that the magnetic field associated with a seamount is caused by uniform magnetization of the entire bathymetric feature.

Vacquier (1962) has proposed that such an assumption be used in determining the direction and intensity of magnetization of seamounts by constructing a model from the bathymetry and computing the direction and intensity of magnetization which gives the best fit to the observed magnetic field. However, if the primary source of the magnetic field observed over a seamount is an intrusive body associated with the seamount, such a procedure could yield quite erroneous results. Evidence for such a situation has been reported for at least one seamount in the South Atlantic (Hadley, 1964). Computations by the authors (unpublished) show that several seamounts to the west of the Hawaiian Islands have dipole anomalies associated with them which cannot be explained by a constant direction and intensity of magnetization of the entire seamount with its low dipping slopes.

A second point brought out by the present study in connection with interpretation of the magnetic field of submarine volcanic features is this: if highly magnetic intrusive rock is present, age dates or magnetic measurements made on dredged or cored flow material need not necessarily be related to the direction of remnant magnetization obtained from measurements of the magnetic field as obtained on a shipboard or airborne magnetic survey.

#### ACKNOWLEDGMENTS

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# Magnetic Studies of Rocks and Sediments Obtained by Deep Drilling<sup>1</sup>

JOHN C. BELSHÉ

THE MAGNETIC PROPERTIES of the crustal materials which may be drilled in Project Mohole should have many points of geochemical interest. For example, the magnetic susceptibility, the Curie temperature, the magnetic hysteresis, and the magnetic anisotropy may reflect pressure, temperature, and chemical relationships in the crust and upper mantle. In addition, the rocks and sediments may be expected to have a remanent magnetism which has been acquired in the earth's field and may have paleomagnetic significance.

Inasmuch as the average heat flow value in the area of the proposed drilling site is normal, an average conductivity figure of  $2 \times 10^{-3}$  Cal/°C sec yields a thermal gradient value of 70°C/km. Thus, the depth to the magnetic Curie isotherm typical for oceanic basalts can be expected to lie more than 8 km below the surface of the sediments—too deep to be reached by the drilling operation. For most of the material encountered during drilling, we can therefore expect a remanent magnetism which is controlled by the cooling of the material through the Curie point as it formed, that is to say, a thermo-remanent magnetization. In the sediment overlying the crustal rock there may be such magnetizations produced by heating from below, but, in addition, there will be some sedimentary acquired magnetism. Previous work of the writer on exactly such material has shown that it may be of great importance to our understanding of past changes in the geomagnetic field.

Many workers have contributed to studies of ancient magnetizations in igneous rocks. In Hawaii, Doell and Cox (1961a) and Tarling and McDougall (1963) have made measurements of the magnetism remanent in several lava flows. The Hawaii Institute of Geophysics is preparing to extend such measurements during the coming year. To illustrate how studies such

as this may give support to Project Mohole, we will discuss the studies made on material obtained by the trial drilling off Guadalupe in 1961 on the drilling barge "Cuss II."

In that operation drilling extended to 181 m beneath the sea floor. The final 11 m were drilled in a basaltic rock which was overlain by pelagic clays. The natural magnetic remanence of this basalt showed a reversed polarity and no detectable anisotropy was found in the magnetic susceptibility. Doell and Cox (1961b) have reported studies made on 23 specimens of this material. The writer worked on 5 samples taken from material between 100 and 110 cm into the basalt. These samples showed a high uniformity in direction of the natural magnetic remanence with only a  $\frac{1}{2}^\circ$  scatter in declination values and a  $1\frac{1}{2}^\circ$  scatter in the inclination. Three Curie temperature measurements were made on the material. All indicated a Curie point of  $325^\circ\text{C} \pm 10^\circ$  (Fig. 1). There was no indication of a multiple Curie point pattern in any of the curves. One measurement was conducted under an astatic magnetometer so that the direction of the natural remanence could be observed as heating proceeded. This measurement showed no appreciable change in direction of the remanence as the temperature approached the Curie point.

The Curie point agreed well with petrological examinations of the sample. The rock was a fresh, medium grained, olivine basalt, quite rich in pyroxene. The color of the pyroxene suggested that the mineral was low in titanium, and that this element could therefore account for the low Curie temperature in the titanomagnetite mineral fraction. The petrological description of this rock given by Engel and Engel (1964) fitted well the samples which we examined.

Structural and petrological examination suggested that this basalt had been intruded under some cover of sediment. The amount of cover could not be readily ascertained. This suggested

<sup>1</sup> Hawaii Institute of Geophysics Contribution No. 101.



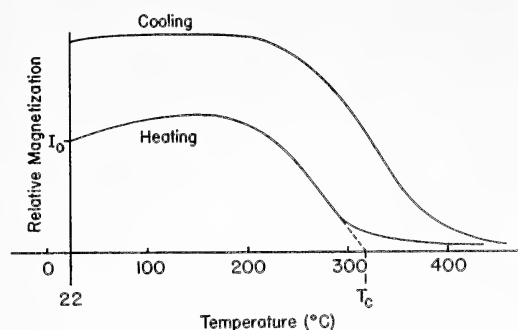


FIG. 1. Pyromagnetization curve established experimentally for the EM 7 basalt.

to us two primary experiments: first, to see if the overlying sediment had been heated sufficiently to acquire a thermo-remanent magnetization; and, second, to determine whether this thermo-remanent magnetization agreed in direction with that of the basalt. If it did so, this would be strong evidence that the whole event had taken place during the period when the main magnetic field of the earth was reversed in polarity from the sense that it has today.

A second study would be to extend the examination for thermo-remanence upward from the contact to see the manner in which it diminished with distance. If intrusion had occurred under a thick overburden, one could expect the thermo-remanent magnetization to give way to a partial thermo-remanent magnetization and the total effect to diminish in an exponential manner. On the other hand, if intrusion had occurred under a very thin overburden of sediment, then the heat pulse from the basalt might well have broken through to the sea floor and been dissipated before any appreciable thickness of sediment had been further deposited in the area. In this case, the upward change of thermal magnetizations would show a discontinuity, diminishing suddenly to the level common for sedimentary type magnetizations. The time scale over which such a cooling might take place and the extent to which temperature isotherms might extend from the basalt could be judged from studies made earlier by Jaeger (1957). Figure 2 is a diagram prepared from such considerations for

the case where the overburden equals the thickness of an intruded sill. It may be seen from this that the 600° isotherm would extend outward to distances of about 20 per cent of the total thickness of the sill. Lower isotherms which could still produce an appreciable partial thermo-remanence might extend out much farther, in excess of half the thickness of the sill. The cooling period would extend over several hundreds of years.

Studies of the sedimentary rock core above the basalt have been hampered for two reasons. First, recovery was very incomplete, particularly in the drill hole which penetrated through the basalt (EM 7). Second, the material was rich in calcareous ooze and had abnormally low magnetic properties as compared with other abyssal sediment. The material placed at our disposal for study was largely confined to Run 3 of the EM 7 drilling. Within this section we had 13 samples ranging from distances of 32 cm above the basalt upwards to a distance of 114 cm. The 6 lowest samples which ranged to distances of 58 cm from the contact showed a positive inclination. The 6 samples overlying this, ranging to a height of 113 cm, had a negative inclination paralleling quite closely that found in the basalt. One positive inclina-

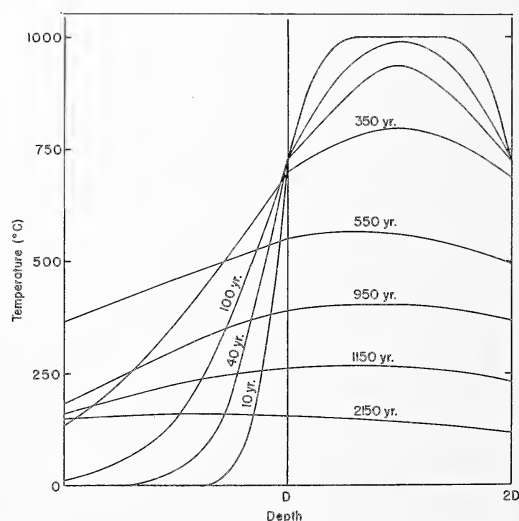


FIG. 2. Change of isothermal lines with time during the cooling of a thick intrusive body.

tion was obtained in the sample taken above this level. Thus, the material which was closest to the basalt and which should have been heated by it to produce a thermo-remanent magnetization in accordance with that of the basalt, did not show this effect.

This pattern of magnetic polarizations presents a paradox. The facts might be interpreted by three hypotheses: (1) The material nearest the basalt might have become unstable, or perhaps was altered by processes emanating from this igneous body, and acquired its field more recently. (2) The positive direction indicates a period of normal magnetizations which was typical of the time at which the basalt was intruded; subsequent to this, a period of reversal occurred during which the overlying reversed materials were laid down and exsolution products in the basalt caused the acquisition of a now reversed remanent magnetization. (3) The reversed magnetization of the basalt may be an example of a spontaneous self-reversal occurring during a period which is better documented by the positive inclination of the immediately overlying and thermally magnetized sedimentary material, remagnetized by the intrusion from its original reversed polarization which is still retained to within 1 m of the contact.

Even on the assumption that the basalt is but little thicker than the maximum depth to which it was penetrated by the drill, we cannot consider the sampling available sufficient to permit a conclusive study of the manner of decrease of thermo-remanent magnetizations away from the contact.

These studies indicate two points that should be taken into consideration in planning any later deep drilling operations. First, it is extremely important for these studies that some attempt be made to orient the core. The writer discussed this point at great length with people in the office of the AMSOC committee (of the Division of Earth Sciences, National Academy of Sciences) during the period of preparation in 1960 for the "Cuss II" operations. Unfortunately, the intent expressed then to orient all cores was not realized. Second, it is extremely important in studies of this type that recovery

be as complete as possible, even in the sedimentary column.

A further matter for consideration has come from studies of these "Cuss II" drill samples. This concerns the consolidation characteristics and porosity of the sediment as studied and reported by Hamilton (1964) and by Moore (1964). Hamilton shows that porosities at the sediment surface were about 80 per cent and that *in situ* porosities for the deepest samples were of the order of 72 per cent. Thus, a reduction of no more than 5 per cent due to overburden pressures could be accounted for even in the deepest sample studies (168 m). Moore shows that the shear strength varied from less than 0.1 kg/cm<sup>2</sup> at the surface to more than 2.8 kg/cm<sup>2</sup> near the basalt.

These findings have two points of importance to studies of magnetism. First, the increase in shear strength seems to be due to diagenetic processes such as cementation and bonding. These processes might be important in the acquisition of chemical magnetizations during the consolidation history of marine sediment, particularly in an area where iron cementation might be expected. Second, these studies in no way support the suggestion made by Keen (1961), working with the writer at Cambridge University, that compaction might produce an inclination error which would increase with burial depth in samples taken by piston coring.

The deep marine magnetic studies being done by the Hawaii Institute of Geophysics, in addition to studies of Hawaiian basalt, should continue to have immediate relevance to the Moho Hole drilling project. Our measuring equipment and techniques are eminently suited to this task. One particular area to which we can contribute comes from the knowledge we have acquired in successfully constructing a photographic recording instrument which can orient a deep-sea sediment core.

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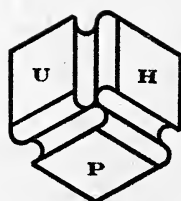
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A QUARTERLY DEVOTED TO THE BIOLOGICAL  
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

LINDA HAITHCOCK PEQUEGNAT

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EDWARD B. CUTLER

*Pogonophora from the Eastern Tropical Pacific*

WALTER T. PEREYRA

*Opisthoteuthis californiana*, the Flapjack Devilfish

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A QUARTERLY DEVOTED TO THE BIOLOGICAL  
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# The Bathypelagic Mysid *Gnathophausia* (Crustacea) and Its Distribution in the Eastern Pacific Ocean

LINDA HAITHCOCK PEQUEGNAT<sup>1</sup>

A NEED HAS LONG EXISTED for an improved collecting device for capturing the larger and more actively swimming bathypelagic animals of the sea. The Isaacs-Kidd Midwater Trawl was developed at the University of California's Scripps Institution of Oceanography in 1950 and has largely satisfied this need (SIO Reference 53-3, 1953).

Bathypelagic specimens have frequently been captured in the deeper hauls of the standard one-meter plankton nets. However, the self-depressing midwater trawl, larger and capable of greater depths (up to 4000 m) and speeds (up to 5 knots) than the standard 1-meter net, has given us more productive samplings of the larger bathypelagic forms (Figs. 1 and 2). In addition, the midwater trawl has captured many species of deep-sea fishes not previously reported in the Pacific as well as species entirely new to scientific literature—forms which apparently have previously eluded capture at these depths by traditional, less effective collecting devices.

The midwater trawl collections made by the Scripps Institution of Oceanography in the eastern Pacific Ocean during the period 1950–53 were examined for the presence of the mysidacean genus *Gnathophausia*, a striking crimson red crustacean conspicuous in midwater trawl hauls from bathypelagic waters. The order Mysidacea has been divided into two subgroups based upon very widely separating morphological characteristics: the suborder Mysida and the phylogenetically more primitive suborder Lophogastrida. *Gnathophausia* is the "giant" genus in the suborder Lophogastrida, containing the largest mysids ever reported. All of the species of *Gnathophausia* are bathypelagic and

are practically never encountered in shallow water.

Specimens of *Gnathophausia* have been described from as early as the Challenger Expedition in 1873–76 (Sars, 1885 and Willemoes-Suhm, 1875), and have been reported from all parts of the world from such other pre-twentieth century expeditions as the *Talisman*, the *Albatross*, the *Oceania*, and the *Investigator*. The *Dana* Expedition in 1928–30 and the *Discovery* Expeditions in the 1920's and 1930's have revealed specimens of this genus in greater numbers and from even more widespread locations throughout the world. Prior to the *Dana* Expedition relatively few specimens of *Gnathophausia* had ever been captured—probably fewer than 100 altogether. A total of 1,051 specimens of *Gnathophausia* were taken by the *Dana*, adding considerably to our knowledge of this group of animals. The distribution and biology of *Gnathophausia* is reported in the greatest detail to date by Fage (1941) in his study of the vast *Dana* collections.

Few studies were made of bathypelagic animals in the eastern Pacific Ocean prior to the development of the midwater trawl and the subsequent collections made by the Scripps Institution during and after its development. Banner (1947) reported on one species of *Gnathophausia* (involving 24 specimens) from the northeastern Pacific off Canada and Alaska, and Banner (1954) discussed the distribution of two species of *Gnathophausia* from collections made off the California coast by the Allan Hancock Foundation. These latter collections involved fewer than 30 specimens of *Gnathophausia* and were taken from shallower levels than those sampled by the midwater trawl.

The development of the midwater trawl at the Scripps Institution has produced a rich collection of bathypelagic specimens, particularly from the eastern Pacific Ocean area. A total of 400 specimens of *Gnathophausia* were availa-

<sup>1</sup> Formerly with the Scripps Institution of Oceanography, University of California at La Jolla, California. Present address: c/o Department of Oceanography, Texas A & M University, College Station, Texas. Manuscript received March 23, 1964.

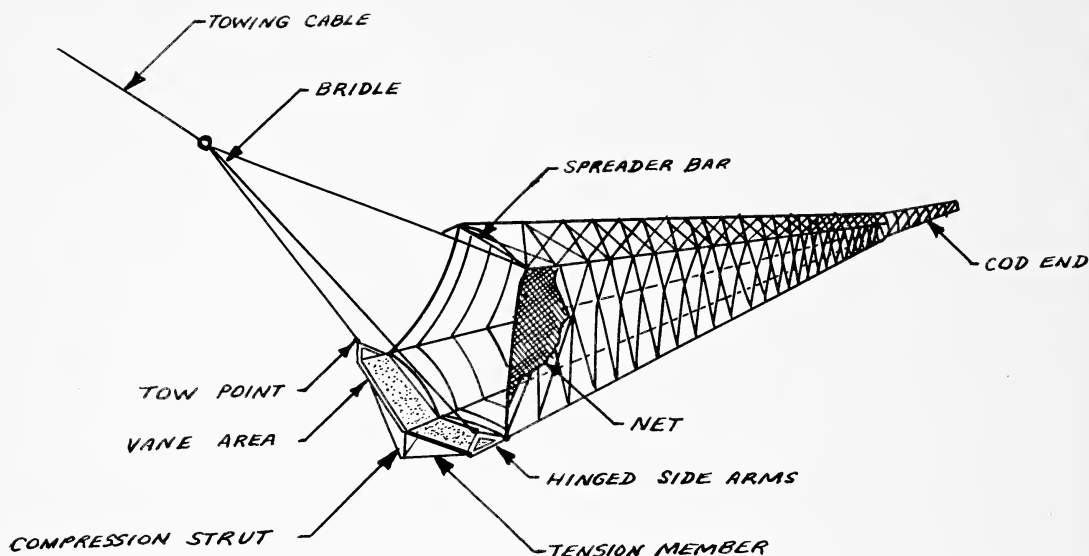


FIG. 1. The Isaacs-Kidd Midwater Trawl. (From SIO Oceanographic Equipment Report, 1953.)

ble for study from the Scripps 1950-53 collections.

In all eight species of *Gnathophausia* are recognized: *G. ingens* (Dohrn), *G. gigas* Willemoes-Suhm, *G. gracilis* W-Suhm, *G. zoea* W-Suhm, *G. elegans* G. O. Sars, *G. longispina* G. O. Sars, *G. affinis* G. O. Sars, and *G. scapularis* Ortmann. Of these eight species, four have been identified in the midwater trawl hauls from the Scripps 1950-53 collections in the eastern Pacific. They are *G. ingens*, *G. gigas*, *G. gracilis*, and *G. zoea*.

#### SYSTEMATIC REVIEW AND MORPHOLOGY

Since the time of Boas' early report (1883) the mysidaceans have been separated from the euphausiaceans into two distinct orders of the crustacean subclass Malacostraca. These two groups had previously been joined in the order Schizopoda (now abandoned) of Latreille (1817). Hansen (1893) and Calman (1904) further agreed with Boas in separating the two groups, allying the Euphausiacea with the Decapoda in the tribe Eucarida and allying the Mysidacea with the orders Cumacea, Tanaidacea, Isopoda, and Amphipoda in the division Peracarida. An excellent review of the historical systematics and nomenclature of the Mysidacea in relation to other crustacean groups

appears in Tattersall and Tattersall (1951), and the reader is referred to this work for the detailed and complete summary.

#### KEY TO SUBORDERS OF MYSIDACEA<sup>2</sup>

1. Branchiae (podobranchiae) present on some or all of the thoracic limbs. Marsupium of seven pairs of brood lamellae. Pleopods in both sexes with both rami multiarticulate and natatory; none secondarily modified in the male. No statocyst on endopod of uropod. . . . . LOPHOGASTRIDA
2. Branchiae (podobranchiae) absent. Marsupium generally of fewer than seven pairs of brood lamellae. Pleopods of male natatory or reduced, one or more pairs usually modified as accessory copulatory organs; pleopods of female reduced to simple undivided plates, not natatory. Statocyst usually present on endopod of uropod. . . . . MYSIDA

The suborder Lophogastrida, with which we are concerned in the study of *Gnathophausia*, is divided into two families: (1) the Lophogastridae containing five genera, *Lophogaster*, *Paralophogaster*, *Chalaraspidium*, *Ceratolepis*, and *Gnathophausia*; and (2) the Eucopiidae with the single genus *Eucopia*.

<sup>2</sup> From Tattersall and Tattersall, 1951.

KEY TO THE THREE MOST COMMON GENERA  
OF THE SUBORDER LOPHOGASTRIDA<sup>3</sup>

1. Branchiae present on all or some of the thoracic limbs. Pleopods well developed in both sexes, natatory, unmodified. No statocyst. Marsupium with seven pairs of brood lamellae (oostegites). . . . . 2
2. Pleural plates of abdominal somites distinct and moderately well developed. . . . . 3
- 2'. No pleural plates on abdominal somites. Outer margin of scale naked. Telson entire. . . . . *Eucopia*
3. Exopod of uropod divided by a suture near the apex. Maxillules with endopod in the form of a reflexed two-segmented palp. . . . . *Gnathophausia*
- 3'. Exopod of uropod undivided; outer margin naked and ending in a tooth. Maxillules without endopod. Antennal scale heart-shaped, outer margin serrated. . . . . *Lophogaster*

*Distinguishing Characteristics  
of the Genus Gnathophausia*<sup>4</sup>

1. CARAPACE: Rather large, only loosely covering the trunk for most of its length, and exteriorly provided with raised longitudinal keels. Posterior part of carapace usually drawn out dorsally into a posteriorly pointing spine (more pronounced in younger than in mature specimens).

2. ROSTRUM: Elongated and spiniform.

3. ANTENNULE: Antennular peduncle short and thick, outer flagellum greatly produced.

4. ANTENNA: Antennal scale of somewhat varying form in different species.

5. EYES: Eyes well-developed with a small papilla issuing from the stalk anteriorly.

6. MAXILLULE: Posteriorly recurved palp on maxillule armed with long setae especially at distal end.

7. MAXILLA: Third segment has a long, well-chitinized lobe which is incised right to its

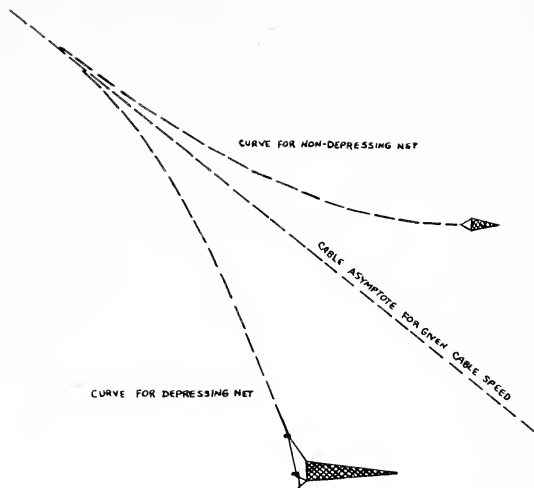


FIG. 2. Comparison of Isaacs-Kidd Midwater Trawl with non-depressing net. (From SIO Oceanographic Equipment Report, 1953.)

base forming two long, slender, finger-like processes armed with setae only at their tips. On the outer side of the coxa there is a brightly pigmented papilla which bears the opening of a gland producing a luminous secretion.

8. THORACIC LIMBS: Maxillipeds with exopodites either very small or entirely lacking. Remaining thoracic limbs nearly uniform, all provided with exopods.

9. BRANCHIAE: Those on second to seventh thoracic limbs divided into four branches with irregularly lobed pinnules. Branchiae on eighth thoracic limb rudimentary.

10. THORACIC STERNITES: In males each thoracic sternite bears a tubercle.

11. ABDOMEN: Abdominal segments narrow with small bilobed epimera. A transverse groove dividing the sixth abdominal segment.

12. UROPODS: External branch broader than internal branch with two segments on external branch.

13. TELSON: Large, constricted near the base; two long keels present on dorsal surface; lateral margins armed with spines arranged in series of larger spines with smaller ones between; apex armed with two strong, curved spines connected at the base to form a backwardly directed crescent.

14. MARSUPIUM: Seven pairs of oostegites.

<sup>3</sup> From Tattersall and Tattersall, 1951.

<sup>4</sup> Compiled from Sars, 1885; Fage, 1941; and Tattersall and Tattersall, 1951.

KEY TO THE SPECIES OF THE GENUS *Gnathophausia*<sup>5</sup>

- a. Antennal scale small, not jointed, no strong rib terminating in a spine on outer margin; outer margin serrate. Epimera of sixth abdominal segment united ventrally, forming together a cordiform, concave plate, incised at apex. Dorsal keel of carapace interrupted. Lower lateral keel not curving upward behind, but terminating in a spine at the postero-inferior angle. Branchiostegal lobe generally with a well developed spine (sometimes obsolete). Maxillipeds with a small exopodite.
  - b. Both lappets of the epimera of the second to fifth abdominal segments pointed and spiniform. Antennal scale subovate, apex shortly pointed. . . . . *ingens*
  - b'. Anterior lappet of the epimera of the first to the fifth abdominal segments small, rounded; posterior lappet pointed and spiniform. Antennal scale sublanceolate, tapering to a sharp spiniform point. . . . . *gigas*
- a'. Antennal scale large, of usual form, jointed at the extremity, outer margin formed by a strong rib terminating in a spine. Epimera of sixth abdominal segment not confluent ventrally.
  - b. Lower lateral keel of carapace not curving up behind, but terminating in a spine on the postero-inferior angle of the carapace. Median keel of carapace interrupted, with spiniform serrations. Median line of abdominal segments with strong spines. Upper lateral keel of carapace wanting. Two epimeral spines on each side of the anterior section of the sixth abdominal segment. Maxillipeds with exopodite. . . . . *gracilis*
  - b'. Lower lateral keel of carapace curving up behind; no spine at postero-inferior angle of carapace. Median keel of carapace not interrupted, without spiniform serrations. Median line of abdominal segments—if armed at all—only with posteriorly projecting, small spines. Upper lateral keel of carapace present, very rarely wanting. Maxillipeds without exopodite.
    - c. Two epimeral spines on each side of anterior section of sixth abdominal segment. Upper lateral keel of carapace present. Antennal spine obsolete. Branchiostegal lobe with a well-marked triangular spine. Spine of outer margin of antennal scale projecting considerably beyond terminal lobe, serrated on both margins. . . . *longispina*
    - c'. One epimeral spine on each side of anterior section of sixth abdominal segment. Antennal spine more or less distinct. Branchiostegal lobe without spine, generally rounded, rarely angular. Spine of outer margin of antennal scale not, or only slightly, projecting beyond terminal lobe.
      - d. Upper lateral keel of carapace present.
        - e. Abdominal segments dorsally slightly keeled, with small, posteriorly projecting spines. Epimera of five anterior abdominal segments pointed posteriorly. Branchiostegal lobe rounded.
          - f. Carapace not suddenly constricted anteriorly and forming no shoulder. Branchiostegal lobes moderately developed. . . . *zoea*
          - f'. Carapace suddenly constricted anteriorly, forming a distinct shoulder in front of the anterior ends of the upper lateral keels. Branchiostegal lobe greatly expanded. . . . . *scapularis*  
(or *zoea* var. *scapularis*)

<sup>5</sup> Based on Ortmann, 1906, with alterations.

e'. Abdominal segments dorsally not keeled, without spines. Epimera of the five anterior abdominal segments rounded posteriorly. Branchiostegal lobe slightly angular. . . . . *affinis*

d'. Upper lateral keel of carapace wanting. Branchiostegal lobe rounded or angular, but without spine. Abdominal segments dorsally without keel, but posteriorly with a small, depressed triangular projection. Epimera of five anterior abdominal segments ending in small points posteriorly. . . *elegans*

SIZE AND SEXUAL MATURITY

*Gnathophausia ingens* (Dohrn 1870)  
Figs. 3 and 4

- Gnathophausia calcarata* G. O. Sars, 1885
- " *bengalensis* Wood-Mason, 1891
- " *doryophora* Illig, 1906

A total of 204 specimens of *Gnathophausia ingens* were identified from the Scripps 1950-53 collections, consisting of 112 females, 23

males, and 69 juveniles, ranging in size from 25 mm to 139 mm body length (Table 1). The 15 largest specimens (all greater than 110 mm as measured from the level of the eyes to the end of the telson) are listed in Table 2. The body length is normally measured from the base of the rostrum at the level of the eyes to the end of the telson. However, in many cases in past literature, measurements are given which include the rostrum. This latter measurement of total length is less reliable because of dam-

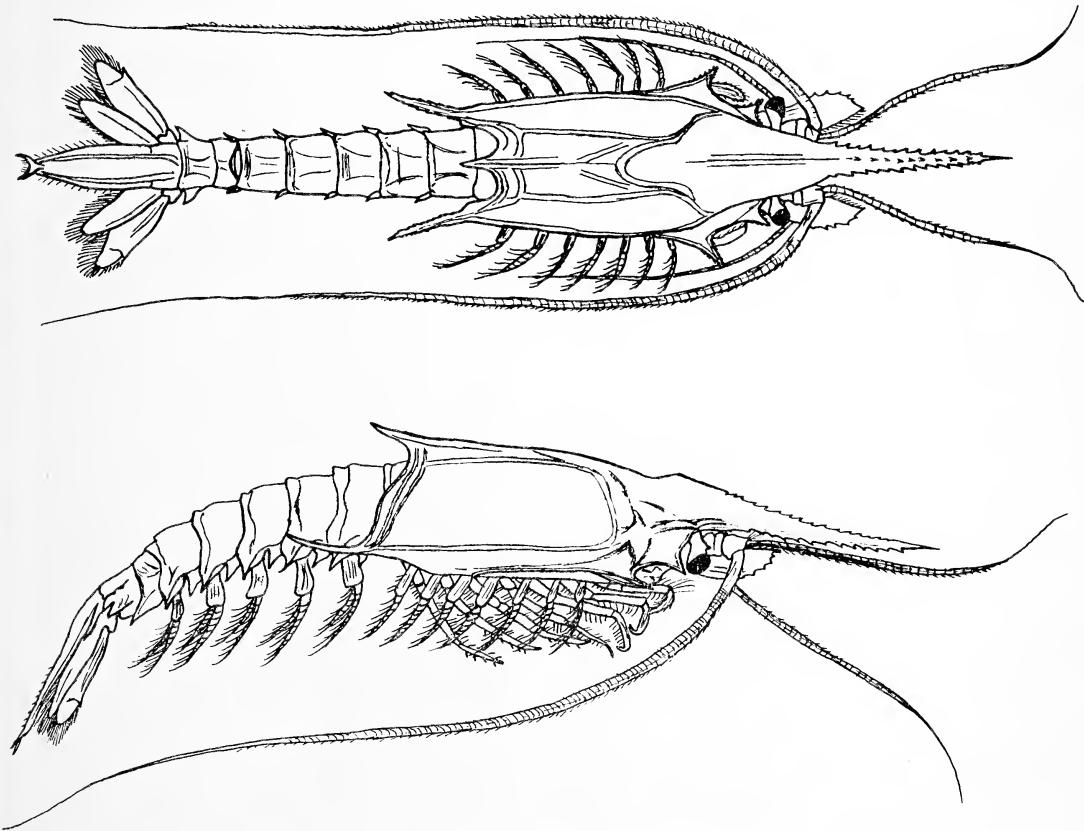


FIG. 3. *Gnathophausia ingens*, young specimen of 98 mm total length. (From Sars, 1885.)



H51-161	4/27- 28/51	30°00'- 29°39'N	121°00'- 121°09'W	2085	3658	2220-0850	1	—	—	—	1	1	2	—
H51-162	4/28/51	29°35'- 29°33'N	121°06'- 121°15'W	914	3658	0940-1600	1	6	4	—	—	1	4	—
H51-167	5/10/51	31°42'- 32°49'N	117°35'- 117°43'W	549	914	1830-2115	12	20	—	—	—	—	—	—
H51-187	5/21/51	32°54'- 33°02.5'N	117°47'- 117°56'W	274	914	2155-2358	3	—	—	—	—	—	—	—
H51-278	7/27/51	32°31.2'- 32°28.4'N	117°45.6'- 117°44.6'W	320	1390- 1463	0100-0251	1	2	—	—	—	—	—	—
H51-355	8/ 6/51	40°22'N	139°23'W	3400	4206	0020-0930	—	—	—	—	1	—	—	—
H51-357	8/ 8/51	40°37'N	143°25'W	3987	4536	0007-0710	—	—	—	1	—	—	—	—
H51-361	8/16/51	51°35'N	150°00'W	1100- 1600	4755	0820-1333	—	—	—	6	—	—	—	—
H51-362	8/16- 17/51	52°48'N	150°10'W	1020	1225	2320-0325	—	—	—	16	—	—	—	—
H51-364	8/21/51	53°35'N	144°20'W	1280	988- 1372	0605-0815	—	—	—	2	—	—	—	—
H51-366	8/24/51	56°15'N	144°50'W	2972	3658	0300-0831	—	—	—	7	2	1	—	—
H51-367	8/25/51	56°20'N	145°20'W	603	768	0400-0530	—	—	—	5	—	—	—	—
H51-371	9/ 5- 6/51	48°58.3'- 48°37.4'N	157°49.8'- 157°29.0'W	4023- 4389	4883	1800-0505	—	—	—	8	1	1	—	—
H51-373	9/ 9- 10/51	41°20.2'- 41°12.5'N	155°13.3'- 155°11.0'W	2140	?	1650-0355	—	—	—	2	1	—	—	—
H51-375	9/15/51	31°54.3'- 31°36.5'N	152°21.6'- 152°03.6'W	3274	5121	0505-1650	1	1	—	—	1	1	1	—
H51-376	9/18- 19/51	30°25'- 30°31'N	145°08'- 144°53.2'W	402	4755	2105-0225	2	—	—	—	—	—	—	—
H51-377	9/23- 24/51	30°01'- 33°09'N	127°39'- 127°34'W	3914	4755	1630-1030	—	1	—	—	—	2	3	—
H51-392	11/ 2/51	32°39.3'- 32°49.4'N	117°37.2'- 117°45.2'W	914- 1097	?	1335-1812	9	2	—	—	—	2	2	—
H51-397	11/ 3/51	32°42.7'- 32°36.4'N	117°37.2'- 117°36.4'W	823- 1042	1170	0655-1053	5	1	—	—	—	4	—	—
H51-406	11/29- 30/51	27°17.6'- 26°56.8'N	117°04.9'- 117°00.9'W	2926	3658	1910-0750	2	1	—	—	—	5	2	—
H52-10	2/26/52	32°37'N	117°37'W	960	1097	?	—	4	—	—	—	—	—	—
H52-13	2/27/52	32°37'N	117°37'W	?	1225	1915-2400	—	1	—	—	—	—	—	—
H52-15	2/28/52	32°17.6'N	117°37'W	?	1207	0835-1300	—	1	1	—	—	—	—	—
H52-32	3/21/52	32°35.5'N	117°28.2'- 117°32.2'W	732	1189	1326-1415	3	7	1	—	—	—	—	—
H52-40	4/ 2/52	33°46'- 33°48.7'N	119°34.3'- 119°39.5'W	1463	1829	1207-1700	1	—	—	—	—	—	—	—
H52-309	5/23/52	17°48'- 17°42'N	124°07'- 124°05.1'W	1105	4271- 1920	0700-1215	—	1	3	—	—	—	7	—



TABLE 1 Continued

STATION	DATE	POSITION		DEPTH OF HAUL (meters)	BOTTOM DEPTH (meters)	TIME	NUMBER AND SIZE (mm) OF INDIVIDUALS								
		Latitude	Longitude				<i>Gnathophausia ingens</i>			<i>Gnathophausia gigas</i>			<i>Gnathophausia gracilis</i>		
							Small <60	Medium 60-100	Large >100	Small <60	Medium 60-100	Large >100	Small <60	Medium 60-100	Large >100
H52-338	6/ 7/52	00°17.7'- 00°42.0'N	110°26'- 110°12'W	1280	3823	0545-1145	—	—	—	—	—	—	15	—	—
H52-363	7/ 1/52	06°58'S- 06°48.5'S	88°35'- 88°30'W	1463	2195	0840-1439	—	—	—	—	—	—	1	—	—
H52-367	7/ 4/52	04°04'- 03°52'S	82°14'- 82°14'W	1641	3658	0450-1050	—	—	—	—	—	—	1	—	—
H52-404	8/ 8- 9/52	01°43'- 01°49'S	89°52'- 90°00'W	1016	2560- 2972	1944-0145	—	—	—	—	—	—	4	—	—
H52-409	8/11- 12/52	01°01.5'- 00°55.0'N	91°45.7'- 91°30.5'W	938- 1108	2286	1816-0017	—	—	—	—	—	—	1	—	—
						TOTALS	87	94	23	50	11	5	58	64	6
							204			66			128		

age or breakage to the rostrum which frequently occurs during sampling and preservation of the specimens.

The largest specimen of *G. ingens* on record is a giant female measuring 350 mm total length (from the tip of the rostrum to the end of the telson). This specimen was captured with the Isaacs-Kidd Midwater Trawl in 1955 on the Scripps Institution of Oceanography's Eastropic Expedition in the equatorial Pacific and was described by Clark (1961). This giant specimen is more than 1½ times larger than the previously reported largest specimen, a male from the Talisman Expedition (Hansen, 1927) with a body length of 185 mm (210 mm total length including the rostrum) which was taken in the Atlantic Ocean south of the Azores. None of the specimens from the 1950-53 Scripps collections in the eastern Pacific exceeded these lengths. The largest is a male of 139 mm body length (160 mm including the rostrum).

Of the 204 specimens of *G. ingens* examined from the 1950-53 Scripps collections, none of the 112 females possessed a completely developed brood pouch. Although many of the larger specimens possessed oostegites as long as or longer than the thoracic legs, none was completely developed to form a true marsupium containing eggs or embryos.

Only three previous accounts of sexually mature females of this species have been reported. One was described by G. O. Sars (1885) from the Challenger Expedition and measured 157 mm total length. A second, described by Fage (1941) from the Dana Expedition, measured 140 mm (165 mm including the rostrum). The oostegites on the latter specimen were clearly longer than the thoracic legs and measured 50 mm in length and 18 mm at their greatest width. The third was the giant female specimen described by Clark (1961).

The criterion used for the determination of sexual maturity in female mysids is the presence of a well developed marsupium. In the case of the males it is more difficult to recognize sexual maturity because of the difficulty in determining when the male genital pore, located on the last thoracic leg, is mature and functional.

The sizes 140 and 157 mm body length may be considered as the minimum sizes of sexual

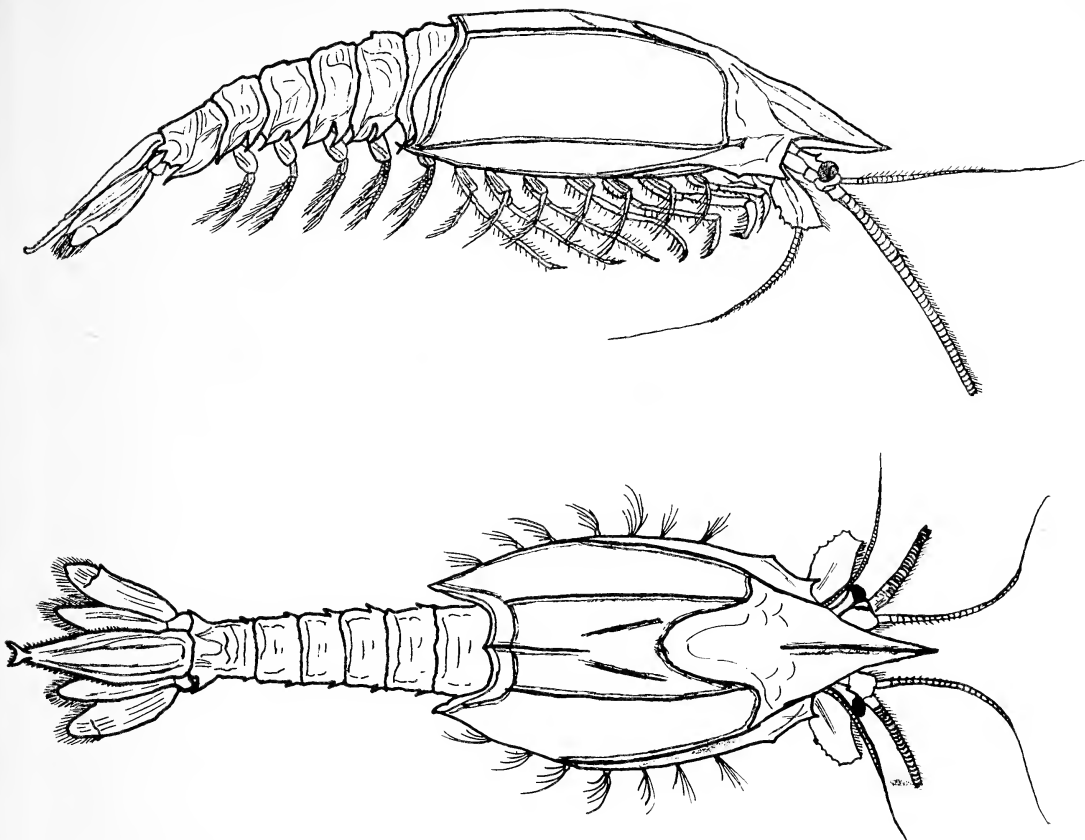


FIG. 4. *Gnathophausia ingens*, adult female of 157 mm. (From Sars, 1885.)

TABLE 2  
*Gnathophausia ingens*  
SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

SIZE (mm)		SEX	STATION*	DEPTH OF HAUL (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
139	160	M	H51-85	549	off Baja California, Mex.
134	155	M	H52-309	1105	off Southern Mexico
125	143	F	H51-162	914	off Baja California, Mex.
123	144	F	H52-32	732	off San Diego, Calif.
123	144	F	H52-15	?	off San Diego, Calif.
122	?	F	H51-162	914	off Baja California, Mex.
120	138	F	H50-277	732	off San Diego, Calif.
118	137	F	H51-90	2213	off Baja California, Mex.
115	138	F	H50-277	732	off San Diego, Calif.
115	134	F	H50-269	750	off San Diego, Calif.
114	135	F	H52-309	1105	off Southern Mexico
114	134	F	H51-85	549	off Baja California, Mex.
113	136	F	H51-45	799	off San Diego, Calif.
113	133	F	H51-45	799	off San Diego, Calif.
111	130	F	H50-277	732	off San Diego, Calif.

\* See Table 1 for exact locations.

maturity in the case of the female *G. ingens*. Fage (1941) reports another female from the Dana Expedition, larger than his sexually mature female of 140 mm, measuring 142 mm (168 mm with the rostrum), in which the oostegites were only 20 mm long and 5 mm wide, i.e., not yet fully formed. Thus there seems to be a range for the size at which sexual maturity occurs in *G. ingens* with some individuals maturing at a smaller size than others.

*Gnathophausia gigas* Willemoes-Suhm, 1875  
Fig. 5

*Gnathophausia drepanophora* Holt and  
Tattersall, 1905

A total of 66 specimens of *Gnathophausia gigas* were identified from the 1950-53 Scripps collections: 10 females, 9 males, and 47 juveniles, ranging in size from 21 to 142 mm body

length. Table 3 presents information about the 5 specimens of *G. gigas* greater than 100 mm in body length.

The male of 164 mm total length (142 mm body length) from Station H51-355 is slightly larger than the previously reported largest specimen, a female of 160 mm total length (Tattersall, 1914). The next largest previously reported specimens were 2 females of 135 mm and 133 mm total length described by Nouvel (1943).

A single female measuring 105 mm body length from Station H51-366 possessed brood lamellae which were well developed into a completely formed brood pouch. The marsupium was empty, however, the embryos evidently having been recently discharged. The brood lamellae measured 27 mm in length and 8 mm at their greatest width. This mature female specimen was captured at a depth of 2972 m over a bottom depth of 3658 m. It has been

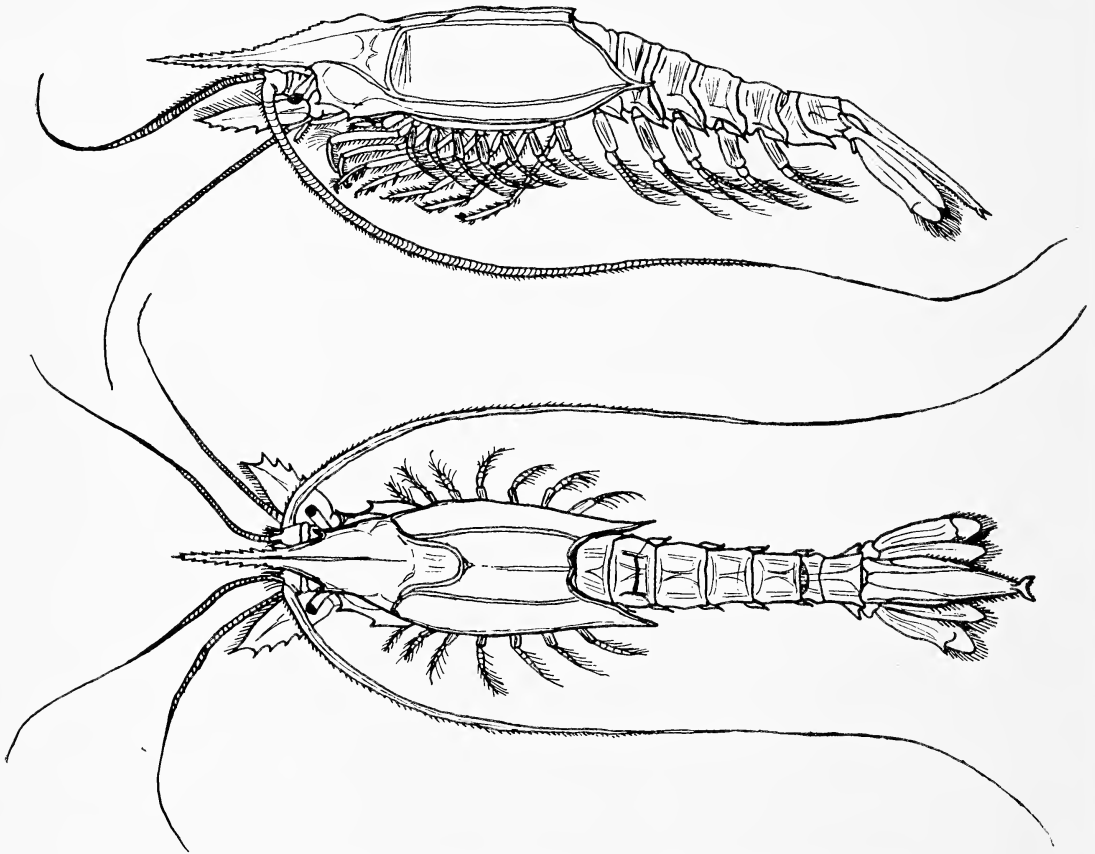


FIG. 5. *Gnathophausia gigas*, adult male of 142 mm. (From Sars, 1885.)

postulated by some that this species and possibly other species of *Gnathophausia* approach the bottom at sexual maturity, thus accounting for the difficulty in obtaining mature specimens with the traditional pelagic nets. It appears, however, that this mature specimen was not near the bottom, having been taken at least 600 m from the bottom when captured with the midwater trawl during the early hours of the morning (from 0300 to 0831 hours).

The minimum size for sexual maturity in this species is probably around 120 mm total length. Ortmann (1906) reports a female of 119 mm total length with fully developed oostegites forming a marsupial pouch. This is the smallest known sexually mature female of this species. On the other hand, the large female of 145 mm total length from the Scripps collections did not possess a fully developed marsupium. Apparently there is a range of size at which sexual maturity occurs, and it is a wide range in this species.

*Gnathophausia gracilis* Willemoes-Suhm, 1875  
Fig. 6

- Gnathophausia brevispinis* Wood-Mason, 1891.—Faxon, 1895
- " *dentata* Faxon, 1893
- " *bidentata* Illig, 1906

A total of 128 specimens of *Gnathophausia gracilis* were identified from the Scripps 1950–53 collections: 64 females, 27 males, and 37 juveniles, ranging in size from 22 mm to 115 mm body length. Table 4 lists the individuals

greater than 100 mm in body length. All 6 of these specimens are larger than the largest ones reported in previous literature. The nearly 250 specimens of *G. gracilis* gathered on the Dana Expedition and reported by Fage (1941) range in size from 20 mm to 100 mm. The 3 largest Dana specimens (2 males and 1 female, each measuring 100 mm in body length) all came from the western Atlantic Ocean in the vicinity of the Caribbean Sea.

The single specimen from the Challenger Expedition described by Sars (1885) measured 41 mm total length (including rostrum). The 2 specimens from the Gulf of Bengal studied by Wood-Mason (1891) were immature and measured 83 mm and 92 mm total length. The John Murray Expedition collected 8 specimens from 22 to 78 mm in length. The Discovery Reports (Tattersall, 1955) list 3 specimens from 24 to 58 mm in size.

Fage (1941) states that the size at which *G. gracilis* reaches sexual maturity is greater in the Atlantic and Indian Oceans than in the Pacific; in the latter, especially the eastern Pacific, there exists a relatively dwarf form of *G. gracilis*. He cites a small female of 52 mm taken in the Gulf of Panama on the Dana Expedition with a completely developed marsupium containing embryos. Fage indicates that there is no evidence that the adults of *G. gracilis* abandon their pelagic life in order to approach the bottom at the time of sexual maturity, and he shows that completely adult females were numerous at all levels in the pelagic fishings of the Dana. The smallest female adult

TABLE 3  
*Gnathopausia gigas*  
SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

LENGTH (mm)		SEX	STATION*	DEPTH OF CAPTURE (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
142	164	M	H51-355	3400	off Northern Calif.
126	145	F	H51-161	2085	off Baja California, Mex.
110	?	F	H51-90	2213	off Baja California, Mex.
105	127	F	H51-366	2972	off Alaska
102	125	M	H51-371	4023-4389	off British Columbia

\* See Table 1 for exact locations.

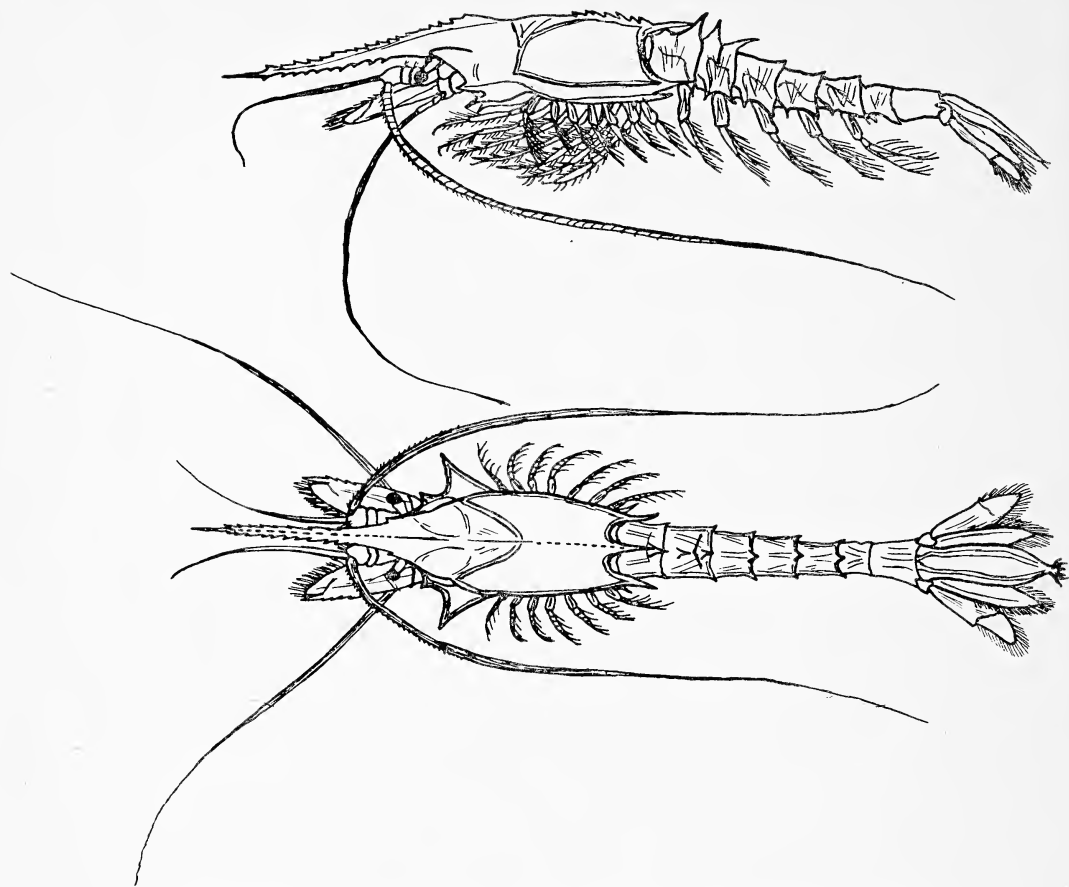


FIG. 6. *Gnathophausia gracilis*, young male specimen of 41 mm. (From Sars, 1885.)

with a completely formed brood pouch taken by the Dana also comes from the Gulf of Panama and measures 49 mm body length. Fage also points out that females of this size from the Caribbean Sea have only rudimentary oostegites and reach their sexual maturity at a larger size. The large female specimen taken from the Gulf of Bengal (Wood-Mason, 1891), measuring 92 mm total length, had incompletely developed brood lamellae which measured only 3 mm in length.

None of the 5 large females of greater than 100 mm body length from the Scripps collections possessed a completely formed brood pouch.

*Gnathophausia zoea* Willemoes-Suhm, 1875

*Gnathophausia Willemoesi* G. O. Sars 1885

" *Sarsi* Wood-Mason, 1891

" *cristata* Illig 1906

Only 2 specimens of *Gnathophausia zoea* (1 male and 1 female) were found in the Scripps 1950-53 collections. Both were taken at Station H52-404, located just south of the equator at  $1^{\circ}43'S$ ,  $89^{\circ}52'W$  to  $1^{\circ}49'S$ ,  $90^{\circ}00'W$ . The depth of the haul was 1016 m, over a bottom depth of 2560 to 2972 m. In addition 4 other specimens of *Gnathophausia* (all *G. gracilis*) were taken at this station, which was occupied during the time interval from 1944 to 0145 hours on August 8-9, 1952. The female *G. zoea* measured 48 mm body length (approximately 70 mm including the rostrum). The male measured 41 mm body length (67 mm with the rostrum). This species is rarely taken off the west coast of North America.

*Gnathophausia zoea* has a wide horizontal distribution, occurring from the Arctic Circle to the Equator. It is especially widespread in

the Atlantic Ocean and in the area of Indonesia in the South Pacific. Fage (1941) has contrasted its wide distribution in the Atlantic with its localization in the tropical zone in the Pacific.

Fage also points out that this species is less strictly bound to the great depths, occurring in a wide range of depths (from 200 m to 3000 m in the captures of the Dana Expedition). The 2 specimens from the Scripps collections came from approximately 1000 m.

#### HORIZONTAL DISTRIBUTION

The Scripps 1950–53 collections studied here were obtained from the eastern Pacific Ocean within an area extending to 160°W and between 60°N and 10°S. Figure 7 shows the locations of captures of the three species of *Gnathophausia* predominant in the collections.

The more northerly species in the eastern Pacific is *G. gigas*, occurring mainly north of 30°N. South of 40°N *G. ingens* takes over, ranging south to approximately 20°N. Below 20°N there is only one station (Station H52–309) where *G. ingens* was identified from the Scripps collections, with the exception of the "giant" specimen of *G. ingens* described by Clark (1961), which was captured in 1955 between 7°50'N, 120°13'W and 8°12'N, 119°54'W.

*G. gracilis* overlaps the distribution of *G. ingens* between 20°–40°N and is the predominantly tropical form occurring in equatorial samples where neither of the other two species was found.

#### *Gnathophausia ingens*

The worldwide occurrence of *G. ingens* falls generally between 40°N and 40°S. Within these limits we find some interesting variations in distribution in different portions of the world's oceans.

Figure 8 shows that *G. ingens*, although scarce in equatorial waters of the eastern Pacific Ocean, is abundant in equatorial waters in other oceans. Fage (1941) comments on the rarity of this species east of the Samoan Islands in the eastern Pacific Ocean, as indicated by the captures of the Dana and previous expeditions. He speculates on the low oxygen tension in this area in the deep-water habitat of the species as being responsible for this lack of specimens. On the contrary, I have found that, off the coasts of California and Baja California, between 20°–40°N, *G. ingens* is the most abundant species of *Gnathophausia* in the Scripps collections taken from this portion of the eastern Pacific. It is more than twice as abundant in our captures from this region as is *G. gracilis*, and 18 times as numerous as *G. gigas*. *G. ingens* is, however, notably absent from our stations occupied in the equatorial zone where *G. gracilis* is the dominant species (Fig. 7). Whether *G. ingens* again becomes more abundant between 15° and 40°S in the eastern Pacific is only speculation until samples can be studied from collections made in these areas. The samples studied here did not extend beyond 8°S (Station H52–363).

Possibly temperature is a factor in this dis-

TABLE 4

#### *Gnathophausia gracilis*

#### SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

SIZE (mm)		SEX	STATION*	DEPTH OF HAUL (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
115	136	F	H51–84	914	off Baja California, Mex.
113	138	F	H51–77	1810	off Baja California, Mex.
113	134	M	H51–90	2213	off Baja California, Mex.
106	120	F	H51–77	1810	off Baja California, Mex.
105	?	F	H51–91	2012	off Baja California, Mex.
103	122	F	H51–90	2213	off Baja California, Mex.

\* See Table 1 for exact locations.



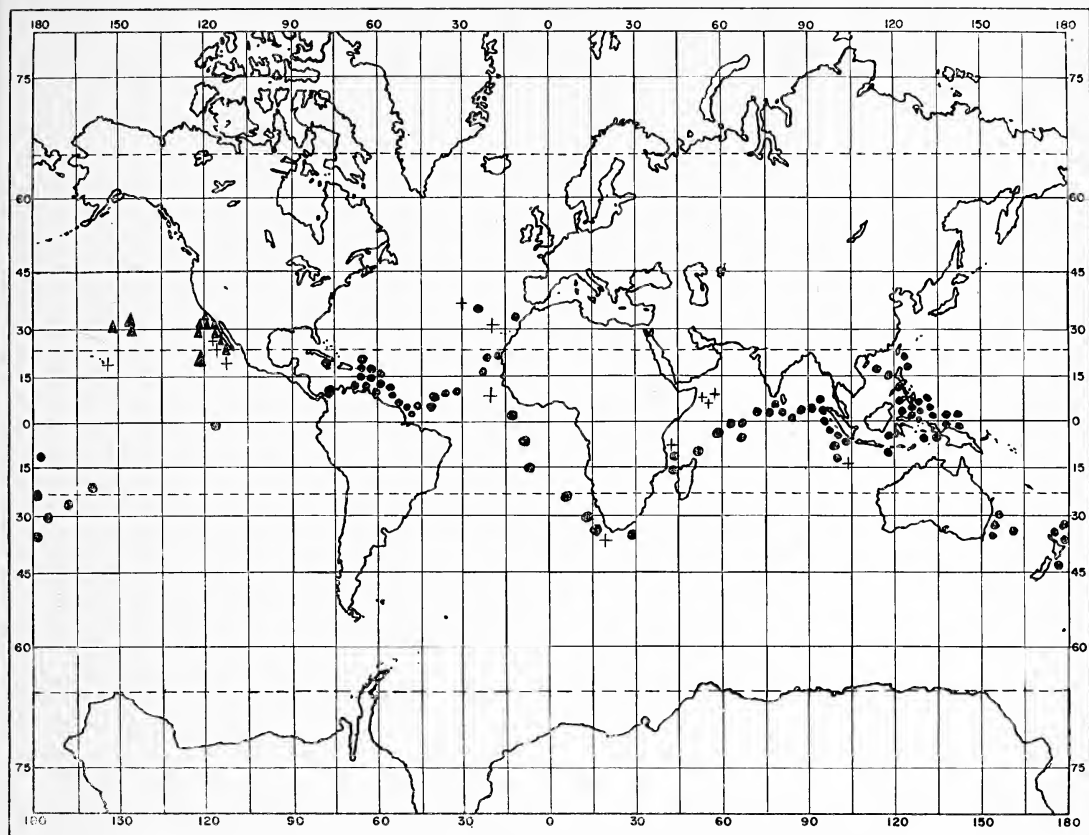


FIG. 8. Geographical Distribution of *Gnathophausia ingens*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

tribution between 15°N and 40°N in the eastern Pacific, but Figure 8 shows that the distribution of *G. ingens* in the other oceans (especially in the Atlantic) and in other portions of the Pacific is not restricted to these latitudes. In the western Pacific and in the Indian Ocean this species is frequently found in the equatorial zones.

Figure 8 further shows that *G. ingens* occurs at mid-latitudes (between 20°-40°N) and is rare in the lower latitudes in the eastern portions of both the Atlantic and Pacific oceans. And, conversely, the species is more abundant in the lower latitudes and rare in mid- and higher latitudes in the western portions of both oceans. Fage (1941) correlates this strange distribution in the Atlantic with temperature isotherms at 600 m. He has shown that the distribution of *G. ingens* falls within the zone of

temperatures of less than 10°C, and is excluded from areas of temperatures of greater than 10°C.

#### *Gnathophausia gigas*

The wide latitudinal range of *G. gigas* is shown in Figure 9. This species is found from near the Equator to nearly 60°N in both the Atlantic and Pacific oceans. In the Southern Hemisphere *G. gigas* has been found as far south as 69°S in the Indian Ocean (Tattersall, 1955). In the Scripps 1950-53 collections *G. gigas* was the only species of this genus which was taken north of 35°N in the eastern Pacific, having been found as far north as nearly 60°N. Fage (1941) suggests that this animal prefers the colder waters, and there is evidence that *G. gigas* lives deeper in the oceans where the



superficial waters are warmer and lives in shallower water when these waters are colder, apparently seeking out temperatures in the 4°C isotherm region.

### *Gnathophausia gracilis*

This species, by contrast, is confined to a small latitudinal range between 35°N and 20°S (Fig. 10). Previously only four captures had been made outside the tropical zone (i.e., 23°N to 23°S), these being taken from the Atlantic Ocean. None had been taken north of the Tropic of Cancer in the Pacific. However, of the 128 individuals of *G. gracilis* in the Scripps collections, a total of 99 specimens were found from stations north of the Tropic of Cancer. A great majority of the larger individuals (greater than 80 mm body length) came from north of the Tropic of Cancer, and all of the largest in-

dividuals of greater than 100 mm body length came from north of 23°N, the maximum latitude of occurrence being 33°N. However, compared with the other species of *Gnathophausia*, *G. gracilis* was the most conspicuous species in the Scripps hauls from the tropical regions of the eastern Pacific, with no *G. gigas* and only a few *G. ingens* occurring in collections taken south of the Tropic of Cancer.

Fage (1941) reports that the *G. gracilis* found in the Pacific (especially in the eastern Pacific where, in the Gulf of Panama, the adults captured by the Dana did not exceed 65 mm length) are of smaller size than those of the Atlantic. His largest specimens (2 males and 1 female, each 100 mm in length) came from the Atlantic in the vicinity of the Caribbean Sea, and he believes that sexual maturity is more precocious in the specimens from the Pacific, particularly in the eastern Pacific, where

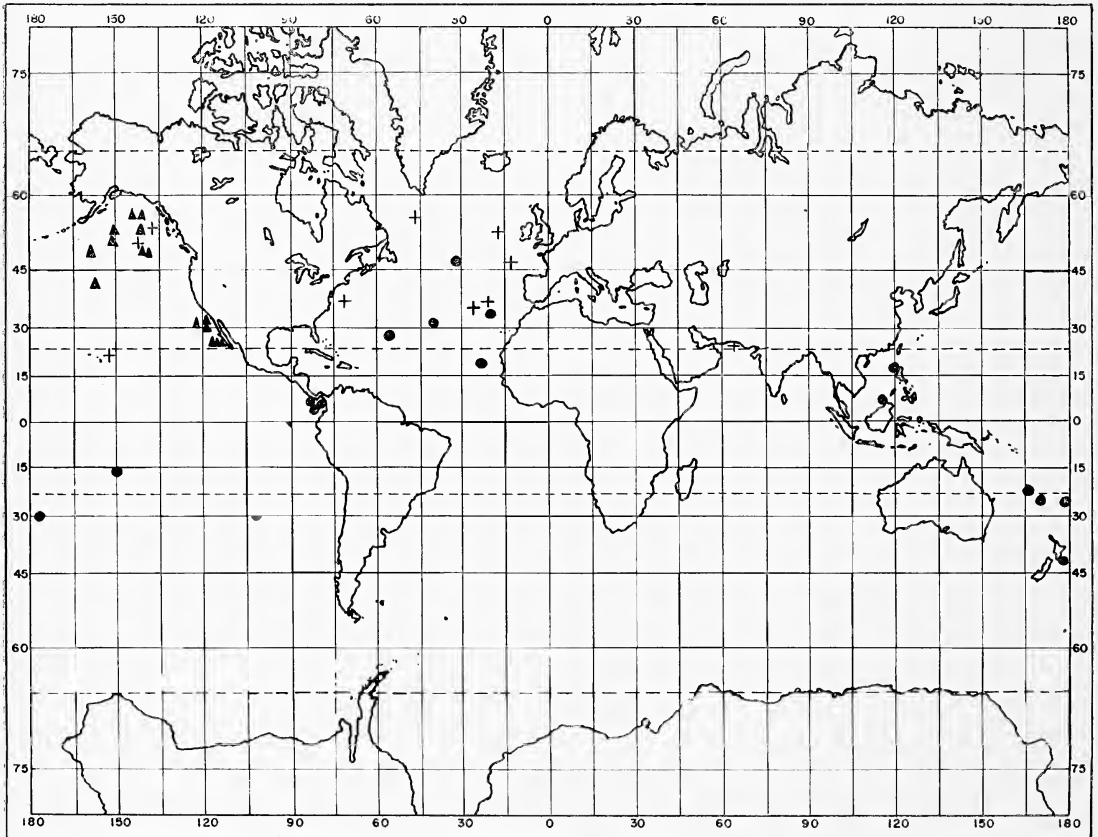


FIG. 9. Geographical Distribution of *Gnathophausia gigas*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

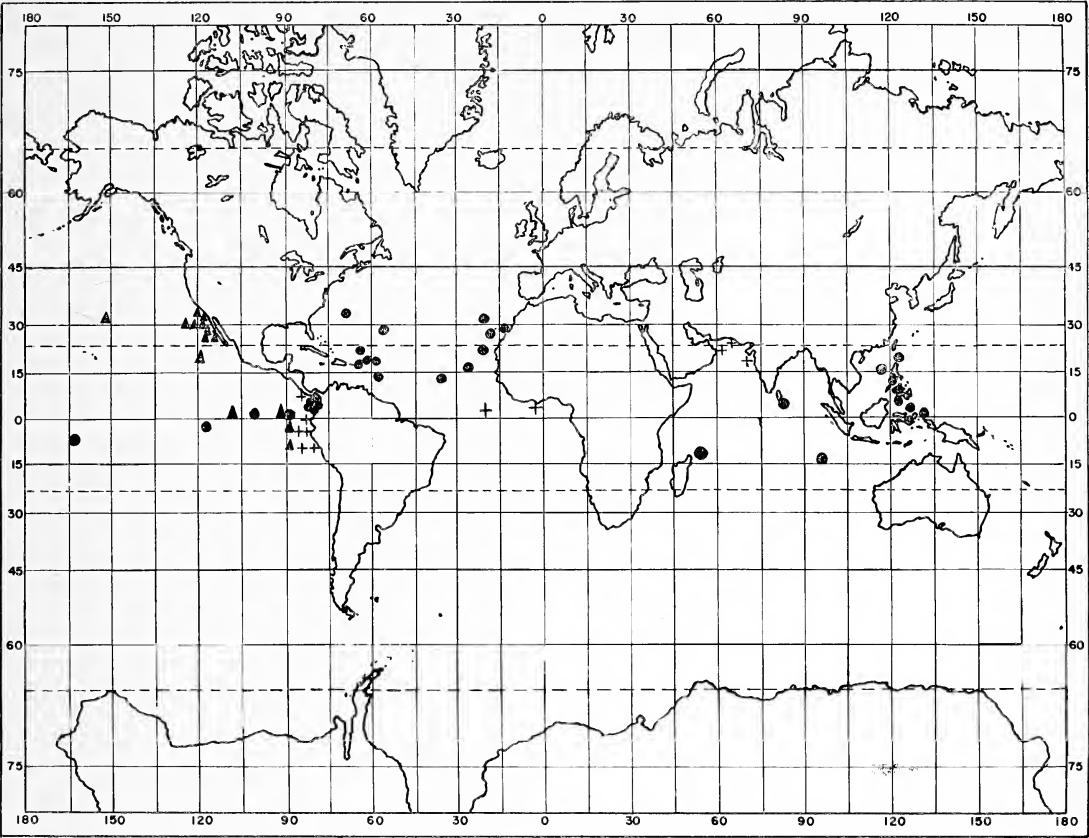


FIG. 10. Geographical Distribution of *Gnathophausia gracilis*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

TABLE 5

DISTRIBUTION OF *Gnathophausia gracilis* ACCORDING TO SIZE IN ATLANTIC AND PACIFIC OCEANS (FROM FAGE, 1941)

NUMBER OF INDIVIDUALS	LENGTH (mm)	ATLANTIC		PACIFIC	
		East	West	East	West
79	50-70	5.0%	2.5%	58.2%	34.2%
14	71-100	7.1%	57.1%	0	35.7%

he found all the adults to be of relatively small size, as shown in Table 5.

Table 6 similarly illustrates the numbers and percentages of the various sized individuals in the Scripps collections taken from two portions of the eastern Pacific: (1) north of 23°N (where Fage lists no captures from the Dana), and

(2) south of 23°N. Thus it can be seen that of the specimens coming from south of the Tropic of Cancer, the majority (75.9%) are less than 80 mm in length (without the rostrum). This percentage actually refers to specimens under 60 mm in length, since no specimens between 61 and 80 mm were found in samples from this southern region in the Scripps collections. From the area north of the Tropic of Cancer the majority of the specimens taken (59.6%) were of the larger size, i.e., greater than 80 mm. Apparently the size difference noted by Fage would not apply to the entire eastern Pacific, but only to that portion within the tropical zone, and particularly in the area of the Gulf of Panama where, indeed, a dwarf form does seem to exist, which reaches sexual maturity at half the size of the normal adult *G. gracilis*.

TABLE 6  
DISTRIBUTION OF *Gnathophausia gracilis* IN EASTERN PACIFIC ACCORDING TO SIZE

EASTERN PACIFIC NORTH OF TROPIC OF CANCER			EASTERN PACIFIC SOUTH OF TROPIC OF CANCER		
Number of Individuals	Length (mm)	Percentage	Number of Individuals	Length (mm)	Percentage
58	<80	59.6	22	<80	75.9
41	81-115	41.4	7	81-115	24.1
Total 99			Total 29		

VERTICAL DISTRIBUTION

The Isaacs-Kidd Midwater Trawl is not equipped with a closing device, so that the exact depth of capture cannot be determined for specimens collected with this sampler. The maximum depth, however, is used as the assumed depth of capture, while recognizing that, although the majority of specimens were most likely captured at the maximum depth where the greatest length of trawling time is spent, there is still the possibility of catching stragglers between this depth and the surface as the net is raised. All depths of capture referred to in this paper have been calculated by measuring the amount of wire played out, then correcting for the wire angle to compute the actual collecting depth of the trawl.

Of the three predominant species of *Gnathophausia* found in the Scripps collections from the eastern Pacific, *G. gigas* is the deepest-occurring (average depth of capture, 2100 m). Another somewhat less deeply-occurring species is *G. gracilis*, with an average depth of capture in the Scripps collections of 1600 m. *G. ingens* occurs predominantly in more shallow waters, where its average depth of capture was 1100 m. A weighted average depth of capture for *G. ingens* was also calculated, taking into consideration the number of specimens captured at each depth. This weighted average depth of 850 m shows that the majority of specimens of *G. ingens* were found at an even more shallow average depth.

Time-depth graphs have been plotted for the three predominant species of *Gnathophausia* found in the 1950-53 Scripps collections (Figs. 11, 12, and 13), in order to detect any possible evidence of nocturnal vertical migrations.

In only one species, *G. ingens*, is there any evidence that the animals are found, in general, in more shallow water during night collections and in deeper water during daytime collections. The graph shows that during the day practically no specimens of *G. ingens* were taken above 650-700 m. On the other hand, the majority of captures at night recovered individuals from the zone between 274 and 650 m. All captures at night from deeper than 650-700 m were from hauls which extended into the daylight period; thus there is the possibility that the specimens were picked up at these deeper levels during the daylight period of towing.

Similar time-depth graphs for *G. gigas* and *G. gracilis* do not seem to indicate any consistent depth differences between daylight and dark sampling. In order to study more precisely the possible existence of nocturnal vertical migration in *Gnathophausia* it would be necessary to employ the use of closing nets to determine more accurately the exact depths of capture. For even more accurate determinations a depth telerecording unit has been employed (Boden et al., 1955).

*Gnathophausia gigas*

Although *G. gigas* tends to occur at greater depths than the other two species, it was occasionally collected in more shallow water (less than 1000 m) than that which Fage (1941) reports as the shallowest depth of occurrence of this species for the captures of the Dana (2000 m depth, 3000 m of wire out). The average depth of capture of *G. gigas* in the Scripps collections was 2100 m, ranging from 600 to 4400 m. Only 3 (19%) of the 16 stations where *G. gigas* occurred were at less than

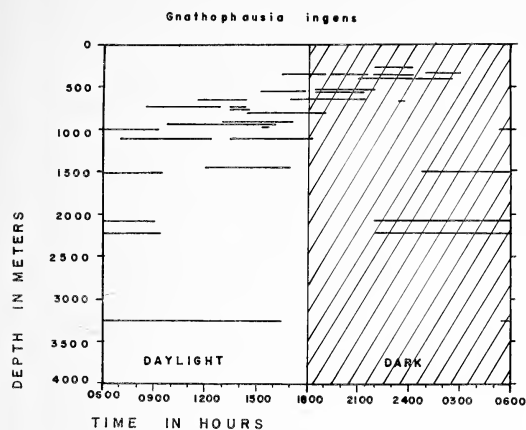


FIG. 11. Captures of *Gnathophausia ingens* plotted according to depth of haul and time of day.

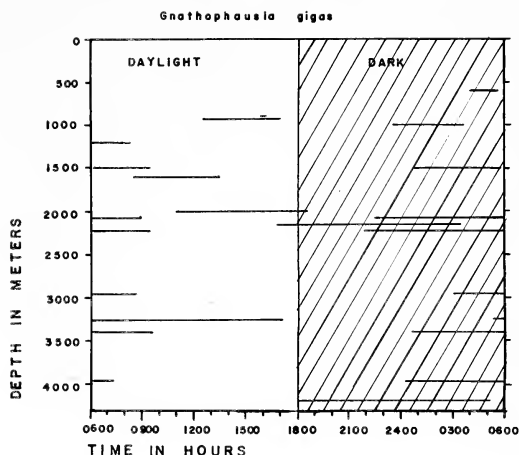


FIG. 12. Captures of *Gnathophausia gigas* plotted according to depth of haul and time of day.

1000 m. This involves 8 individuals (12%) in the total of 66 individuals of this species examined. This compares with 20 of the 34 stations for *G. ingens* (59%) which were at less than 1000 m, and with 5 of the 22 stations (23%) for *G. gracilis*. All specimens of *G. gigas* in the Scripps collections of greater than 100 mm body length came from depths of more than 2000 m.

Closing nets used on the Discovery Expedition (Tattersall, 1955) found immature *G. gigas* at between 650–4000 m depth. Banner (1947) reports on 9 specimens of *G. gigas* from the eastern Pacific off Canada at between 400–1200 m depth, and 15 specimens off Alaska from depths of 300–900 m. These specimens were all smaller than 60 mm body length.

### *Gnathophausia gracilis*

*G. gracilis* has always been described as a species from very deep water (greater than 1500 m). Previous reports show that all records of *G. gracilis* were from depths greater than 1500 m, except for 2 young specimens described by Fage (1941) and Hansen (1927), which were from 800 m. The Scripps collections yielded 30 individuals (collected at 5 separate stations) from depths of less than 1000 m, some of them greater than 100 mm in size.

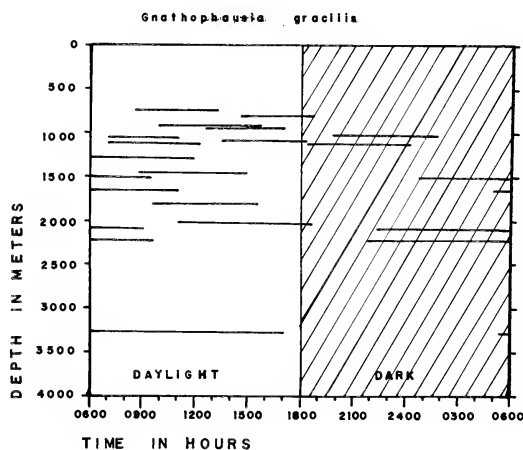


FIG. 13. Captures of *Gnathophausia gracilis* plotted according to depth of haul and time of day.

This amounts to 23% of the total of 128 individuals of this species examined in the Scripps collections. The 2 most shallow depths sampled yielding *G. gracilis* were 732 m (Sta. H50–277), with 1 small male, and 799 m (Sta. H51–45), with 6 juveniles and 3 males. The average depth of capture from the Scripps collections was 1600 m, ranging from 732 to 3914 m.

Fage (1941) suggested that *G. gracilis* maintains itself at a deeper level in the eastern por-

tions of the Atlantic and Pacific oceans than in the western portions mainly in order to escape the zone of low oxygen content. Having studied the temperature, salinity, and oxygen content, he found that in the eastern portions the waters are colder, less saline, and poorer in oxygen content than at the same level in the western portions. Fage listed depths of between 1500 to 2000 m as the zone where *G. gracilis* normally lives. He pointed out that *G. gracilis* is a true bathypelagic species and not a form which lives on the bottom, as was previously believed. A study of Table 1, where the depth of haul and the bottom depth are given for the Scripps collections, also shows this to be true. In all stations where *G. gracilis* was found the depth of capture is from 400 to 2600 m from the bottom. The average difference between the depth of capture and the bottom depth for all positive stations of *G. gracilis* is 1512 m, a considerable distance from the bottom.

#### *Gnathophausia ingens*

*G. ingens*, in contrast to the other two species, occurs in greatest numbers above 1000 m. The average depth of capture in the Scripps 1950-53 collections was 1100 m, ranging from 274 to 3914 m. The majority of specimens were found at an average depth of 850 m (weighted average). Closing nets on the Discovery Expedition (Tattersall, 1955) show that *G. ingens* was most common between 600 and 1500 m, but was also found as deep as 2480-2580 m and as shallow as 210-340 m.

Previous studies have shown that the younger individuals of this species (less than 80 mm in length) are found at more shallow levels than are the larger, sexually mature adults. This is also generally true of the specimens from the Scripps collections. Fage (1941) has found that the peculiarities in vertical distribution, i.e., in certain areas of the Indian Ocean where young individuals were captured at considerably greater depths, can be explained by the vertical distribution of temperatures in those regions. He has found that the depth of occurrence of young individuals of less than 80 mm

length corresponds to depths where the 5°-8°C temperature range occurs. When this temperature occurs deeper, the young individuals occur deeper. He also states that in all the oceans no individual of a size greater than 80 mm has been taken with less than 1000 m of cable immersed, equivalent to an actual depth of 500-600 m. This is generally true of the 1950-53 Scripps collections, with the exception of 2 specimens of 81 and 87 mm body length from Stations H51-75 and H51-76, both taken at a depth of 366 m.

Although only 2 (or 8.7%) of the 23 individuals of *G. ingens* of greater than 100 mm size were taken at less than 600 m (Sta. H51-85), 17 (or 74.9%) of the specimens were from depths less than 1000 m (Table 2).

Fage (1941) states that individuals of *G. ingens* exceeding 80 mm in length are very rare and account for 18% among the captures of the Dana in the Atlantic, for 13% in the Indian Ocean, and only 7% in the Pacific. From the Scripps collections in the eastern Pacific I have found that 26.5% of the individuals were greater than 80 mm in body length. This increase over Fage's figures serves to point out the improved sampling ability of the midwater trawl in deep waters over traditional pelagic nets. Larger and faster swimming specimens are less able to evade capture or to swim out of the nets, due to the greater speed and efficiency of the midwater trawl.

#### PARASITES

Fage (1936, 1940, and 1941) has described a curious protozoan parasite, *Amallocystis fasciatus* (an ellobiopsid flagellate), which occurs occasionally in specimens of *Gnathophausia* (Fig. 14). Of the 1,051 specimens examined from the Dana Expedition, 5 individuals were found which contained this parasite: 3 *G. zoea* and 2 *G. ingens*.

Of the 400 individuals of the genus *Gnathophausia* which I examined from the Scripps collections, I found only 3 parasitized specimens: 2 *G. ingens* and 1 *G. gracilis*. No previous record of parasitism by this flagellate has been reported in *G. gracilis*. This parasit-

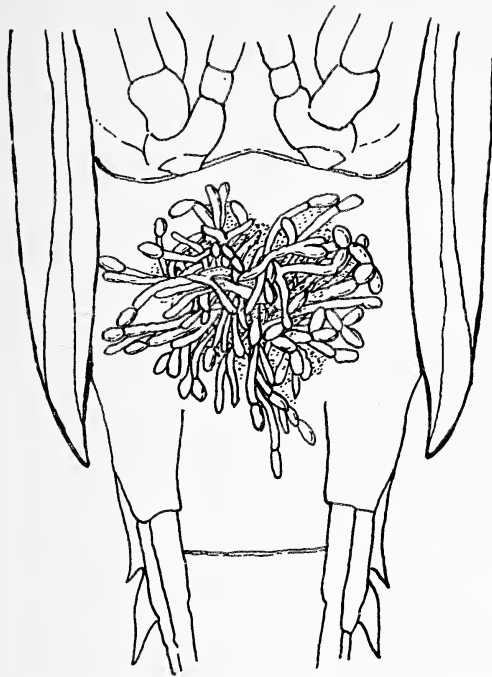


FIG. 14. First abdominal sternite of *Gnathophausia zoea* parasitized by *Amallocystis fasciatus*. (From Fage, 1941.)

ized *G. gracilis* is a female of 70 mm body length (87 mm including the rostrum) and was taken at Station H51-406 at a depth of 0-2926 m. Both parasitized *G. ingens* specimens are females, one of which came from Station H51-406 (from the same haul which captured the parasitized *G. gracilis*) at a depth of 0-2926 m and measured 86 mm body length (102 mm including the rostrum). The other parasitized *G. ingens*, a smaller female measuring 66 mm (82 mm including the rostrum), was taken at Station H52-15, the depth of capture being unknown over a bottom depth of 1207 m. In each case the parasite was attached to the middle of the ventral aspect of the first abdominal segment. Indeed, Fage describes this exact location as being constant among the 5 parasitized individuals which he examined from the collections of the Dana.

Nouvel (1941) also reports on 4 similarly parasitized individuals from the following three species of *Gnathophausia*: (1) *G. ingens*—1 parasitized specimen (a male of 110 mm measured from the antennal scale to the end of the

telson) from the eastern Atlantic off Mogador, Morocco, 0-4000 m; (2) *G. gigas*—1 parasitized female of 115 mm from the Atlantic Ocean south of Spain, 0-4740 m; (3) *G. zoea*—2 parasitized females of 45 and 39 mm from two locations in the eastern Atlantic off Portugal, one at 1241 m, the other at 0-1500 m.

Fage pointed out that the plate of fixation of this parasite is located just under the first abdominal nerve ganglion; and he observed a reaction of the host in the form of a great hypertrophy of this first abdominal ganglion as compared with the other abdominal and thoracic ganglia and with ganglia in normal, non-parasitized individuals.

Another influence of the parasite upon infected females is a retarded development of the secondary sexual characteristics, particularly the oostegites, which were considerably smaller and less well developed in the parasitized females than in non-infected females of the same size and presumably, of the same age. In addition, Nouvel describes an effect on the male *G. ingens*. In this male the sexual orifice is at the base of the last thoracic appendages. In addition this specimen has some very small outlines of oostegites at the bases of all the thoracic appendages except the last pair. This has been described as a "feminizing action" which the parasite exercises on the host.

In the 2 parasitized females of *G. ingens* from the Scripps collections, a retarded development in the oostegites was noted as compared with the normal, non-parasitized females. In both the 66 mm specimen and the 86 mm specimen the oostegites were extremely minute, less than 1 mm in length. A normal female of only 70 mm was found to have oostegites 2 mm in length, and a non-parasitized female of 80 mm possessed oostegites measuring 3 mm.

However, in the case of the parasitized *G. gracilis* of 65 mm which I examined, the oostegites measured 4 mm in length and 1 mm in width. These measurements are similar to those for normal, non-parasitized females of this species of approximately the same length. Thus the parasite does not seem to have retarded the development of the oostegites in this parasitized *G. gracilis*, in contrast to its effects on the other species of *Gnathophausia*.

## SUMMARY

1. A total of 400 specimens of *Gnathophausia* were studied from the Scripps Institution of Oceanography's 1950-53 collections made with the Isaacs-Kidd Midwater Trawl, in the eastern Pacific Ocean, and four species were identified: (a) *G. ingens*: 204 specimens ranging in size from 25 to 139 mm body length (not including the rostrum), taken from a depth range of 274-3914 m, with an average depth of capture of 1100 m; (b) *G. gigas*: 66 specimens ranging in size from 21 to 142 mm body length, taken from a depth range of 603-4883 m, with an average depth of capture of 2100 m; (c) *G. gracilis*: 128 specimens ranging in size from 22 to 115 mm body length, taken from a depth range of 732-3914 m, with an average depth of capture of 1600 m; (d) *G. zoea*: 2 specimens, a female of 48 mm body length and a male of 41 mm body length, taken from a depth of 0-1016 m.

2. The geographical distribution of *G. gigas*, a colder water form, in the eastern Pacific is more northerly (20°-60°N) than is that of *G. ingens* and *G. gracilis*, which occur in warmer waters and exhibit a more tropical distribution, particularly *G. gracilis*.

3. Of the 128 specimens of *G. gracilis* collected 99 were found north of the Tropic of Cancer in the eastern Pacific Ocean, an area where they had rarely been found previously.

4. *G. ingens* was found consistently deeper in daylight hauls than in hauls taken at night, possible evidence for nocturnal vertical migration in this species. No evidence for this phenomenon is shown for *G. gigas* or *G. gracilis*.

5. Among the specimens of *G. gracilis* 6 were greater than 100 mm in body length, the largest measuring 115 mm. All are larger than any *G. gracilis* individuals previously described.

6. A mature female specimen of *G. gigas* measuring 105 mm in body length and having a well developed marsupium is described.

7. A parasitic ellobiopsid flagellate, *Amallocystis fasciatus*, is reported from 2 specimens of *G. ingens* and 1 specimen of *G. gracilis* taken from the eastern Pacific Ocean.

## ACKNOWLEDGMENTS

This study was undertaken at the Scripps Institution of Oceanography in 1955, while I was studying under a National Science Foundation Pre-Doctoral Fellowship under the guidance of Dr. Martin W. Johnson.

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# Pogonophora from the Eastern Tropical Pacific, including Two New Species of *Siboglinum*

EDWARD B. CUTLER<sup>1</sup>

**ABSTRACT:** Two species of Pogonophora are described from the tropical Pacific from a depth of 1354 m. They belong to the genus *Siboglinum* and both are new species, *S. albatrossianum* and *S. ecuadoricum*. Empty tubes of another pogonophore are also described. This material represents the earliest known collection of pogonophores.

THE POGONOPHORAN MATERIAL described below is historically interesting as it was collected in 1888 by the U. S. Fish Commission steamer "Albatross." This was 11 years before the "Siboga" Expedition, whose collections contained the first specimens of this group to be described (Caullery, 1914; Southward, 1961). The "Albatross" material went unnoticed in the U. S. National Museum until 1959, when Dr. F. M. Bayer of the University of Miami discovered it among some pennatulids.

Dr. Fenner A. Chace was good enough to let me borrow it and with the help of Dr. Eve Southward I have been able to describe these new species. I am also indebted to Mr. Grant S. Lashbrook for the illustrations and to Dr. Paul J. Osborne for the use of his microscope.

As this material has been preserved in alcohol for 76 years, it is rather brittle and difficult to work with. Some distortion due to shrinkage is possible but it seems advisable to describe the specimens in spite of this. Other than *Lamelisabella ivanovi* (Kirkegaard, 1961) these are the only pogonophores to be described from this region of the Pacific Ocean. All the material came from "Albatross" Station 2793, and has been deposited at the U. S. National Museum in Washington, D. C.

## Collection Data

LOCALITY: Off Cape San Francisco, Ecuador  
POSITION: 01° 03' N, 80° 15' W

<sup>1</sup> Formerly at Lynchburg College, Lynchburg, Virginia. Present address: Department of Zoology, University of Rhode Island, Kingston, R. I. Manuscript received April 14, 1964.

DEPTH: 741 fathoms (1354 m)  
BOTTOM DATA: green mud, 3.5°C  
DATE OF COLLECTION: 3 iii. 1888

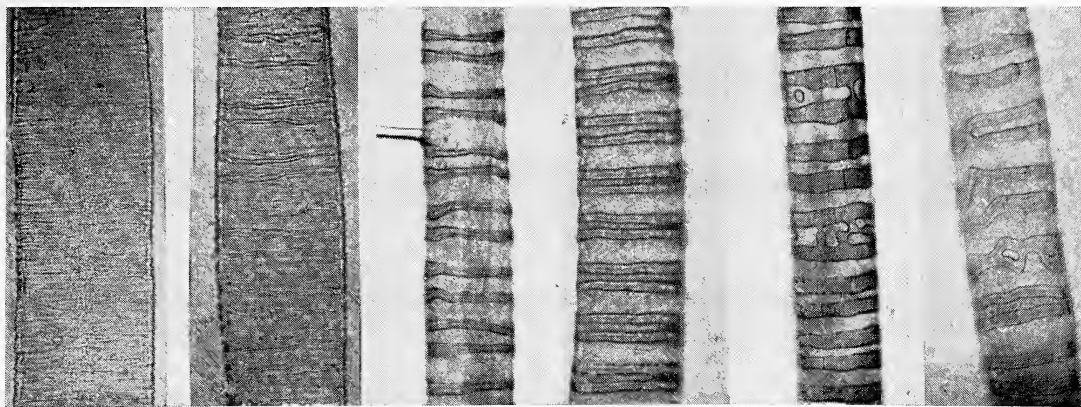
*Siboglinum albatrossianum* sp. nov.  
Figs. 1-6, 13 A-E

HOLOTYPE: USNM 31824; PARATYPE: USNM 31825

**DESCRIPTION:** This species is represented by 47 tubes, 24 containing parts of animals. As the significance of the material was not realized at the time of collection it was probably handled rather carelessly. Consequently, I was unable to find any one animal which was not damaged.

The tubes have the characteristic ringed appearance on the major portion. The anterior and posterior ends are thin, colorless, and wrinkled (possibly from dehydration). This wrinkled appearance is present in the colorless interspaces between the rings on many of the tubes. These interspaces are often pinched or indented and have even imposed a pseudometamerism on the body. The shade of brown in the rings becomes darker and the rings also become longer toward the middle of the tube. The diameter of the tube is 0.11-0.125 mm while the length of the rings is 0.014-0.026 mm, always less than one-fourth the diameter. The rings are paired throughout with frequent connections between the pairs in the middle region. The longest tube in the collection is 90 mm.

One specimen measures 7.9 mm from the anterior end to the first girdle. The width of the trunk varies from 0.09 to 0.12 mm. The forepart (promesosome) is 1.35-1.46 mm long.



FIGS. 1-6. Different regions of the tube of *S. albatrossianum* from anterior to posterior. 1, Clear, limp region. 2, Thin, pale rings appearing. 3 and 4, Lengthening rings in midportion. 5 and 6, Approaching the posterior end, where the rings become more irregular.

The width of the mesosome is 0.09–0.12 mm; the ratio of width to length being 1/12–1/14. The cephalic lobe is small, rounded, appears quite glandular, and lacks a pretentacular groove. Just behind the base of the tentacle there is a groove on the ventral side only. The tentacle measures 35–45  $\mu$  in diameter and bears two rows of pinnules. The length of the pinnules varies but usually exceeds the diameter of the tentacle.

In unstained material the bridles are very difficult to distinguish. After staining with hematoxylin they can be seen as very thin lines which join ventrally but leave a small gap on the dorsal side. There are short, delicate, transverse lines crossing the bridles, as in *S. tenue* (Ivanov, 1963:240). There are no visible glands behind the bridle. The bridle is in the middle of the promesosome.

The metameric glands of the metasome are present but very poorly defined. There are two girdles which are from 0.55 to 0.63 mm apart and each consists of one row of platelets (uncini). The platelets are 11–15  $\mu$  long with two characteristic groupings of small teeth. In the posterior region there are a few scattered papillae. The spermatophores are more or less spindle-shaped and measure about 70  $\mu$  by 7  $\mu$ . I was unable to distinguish their filament.

This species is similar to *S. weberi*, but different in the following aspects: forepart proportionally a little longer, bridle about half way along the forepart, two rows of pinnules,

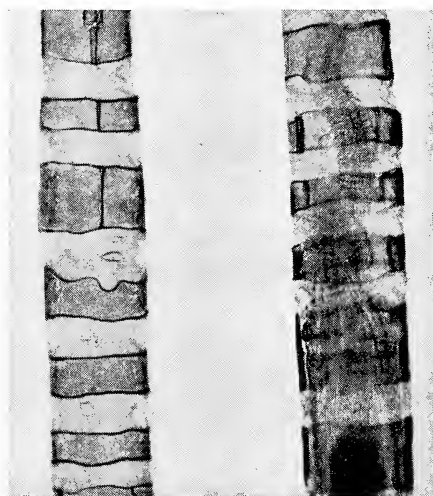
much larger spermatophores, girdles closer together, and more double tube rings. It differs from *S. veleronis* in that the bridle is farther back on the mesosome, the glandular papillae are less well developed, it lacks the cylindrical pores on the sides of the mesosome, and the toothed platelets are of a different type.

*Siboglinum ecuadoricum* sp. nov.

Figs. 7, 8, 13F

HOLOTYPE: USNM 31822; PARATYPE: USNM 31823

DESCRIPTION: This species is represented by two unsegmented tubes, each containing an ani-



FIGS. 7-8. Tube of *S. ecuadoricum*. 7, Middle region. 8, Portion of the tube containing the anterior part of the animal and part of the tentacle.

mal. The longest tube measures 40 mm and the diameter varies from 0.11 to 0.13 mm. One striking feature of this species is the length of the solid, yellowish rings and the interspaces. Most rings measure about 0.05 mm but vary from 0.04 to 0.09 mm long, while the clear spaces are usually about 0.045 mm. The edges of the rings are irregular. The anterior and posterior regions of the tube are clear and there is a short transition area from the ringed to the clear region, rather than a gradual fading out as in the preceding species. There are several species of *Siboglinum* with rings of a comparable length, but either the diameter is larger (e.g., *S. japonicum* and *S. timorensis*) or else they have paired rings or doublets or are more regular in appearance (e.g., *S. pusillum* and *S. hyperboreum*).

The post-annular region is largely missing in both specimens but other measurements are as follows (in mm):

MEASUREMENT	A	B
Anterior girdle to tip of cephalic lobe	6.9	10.8
Distance between girdles	0.91	1.8
Diameter of trunk at girdle	0.116	0.105
Forepart of body: length	0.77	0.69
Forepart of body: width	0.105	0.093
Ratio of width to length of forepart	1/7	1/7

The cephalic lobe is small, rounded, and somewhat flattened. The tentacle is 35–45  $\mu$  in diameter and there are two rows of pinnules present. The length of the pinnules is about equal to the diameter of the tentacle. A post-tentacular groove is present and, in addition, there are two partial grooves, or wrinkles, farther back on the mesosome.

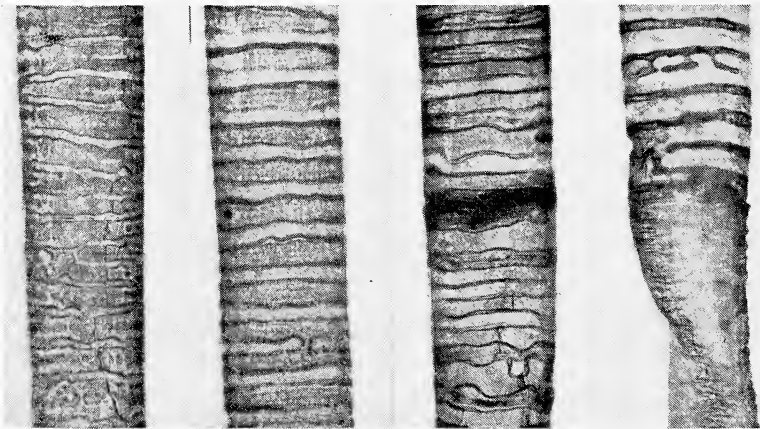
The bridles are colorless and not very distinct. They join ventrally but there is a gap on the dorsal side about  $\frac{1}{4}$  the diameter of the mesosome. There are no other distinguishable features on the pro-mesosome.

The mesosome-metasome division is clear and there are about 30–35 pairs of metameric papillae present, followed by scattered glandular patches. There are two girdles which do not completely encircle the trunk. They are composed of a single row of platelets which are about 13–14  $\mu$  long. The spermatophores are long, thin (about 80  $\mu$  by 7  $\mu$ ), and pointed at both ends. The filament was not observed.

? GEN. ET SP.

Figs. 9–12

A third species is represented by three empty tubes, 15, 18, and 79 mm long. The longest tube is divided into three regions: 2 mm clear and limp, 16 mm of obvious segmentation



FIGS. 9–12. Tube of ? gen. et sp. 9, The abrupt transition from the clear region to that of narrow rings. 10, Anterior section showing dark area where two segments come together. 11, Regular rings in the midportion. 12, Posterior region showing the double nature of the rings with irregular openings between the members of the doublets.

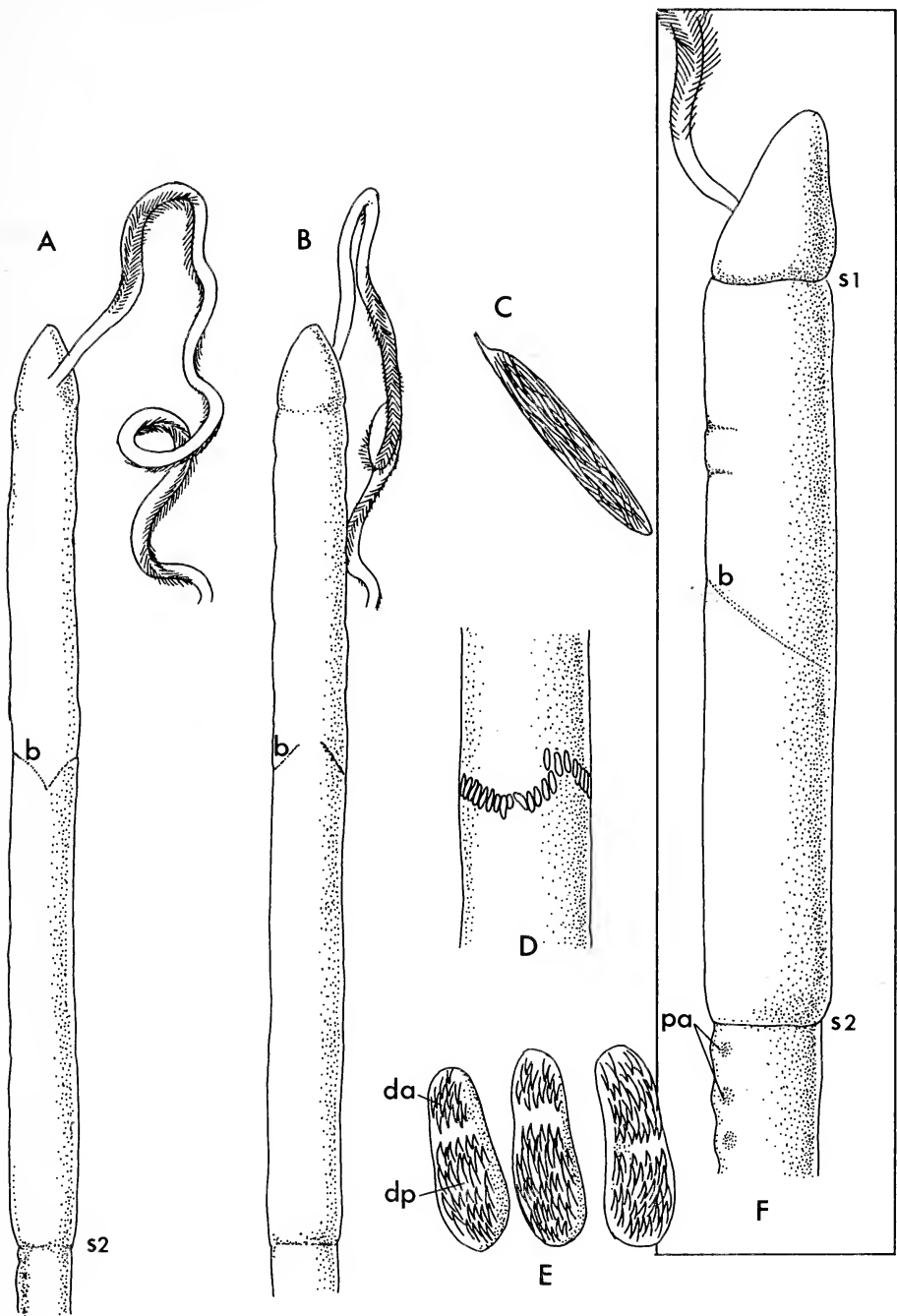


FIG. 13. A–E, *Siboglinum albatrossianum*. A, Forepart of body from ventral side; B, from dorsal side; C, spermatophore; D, region of a girdle; E, toothed platelets.

F, *Siboglinum ecuadoricum*, side view. b, Bridle; da, anterior teeth; dp, posterior teeth; pa, papilla; s<sub>1</sub>, post-tentacular groove (between protosome and mesosome); s<sub>2</sub>, groove between mesosome and metasome.

with rings (mostly unpaired), and a 60 mm ringed portion where the segmentation is not apparent. This breaking down of the segmentation is similar to that of *S. sumatrense*, but the rings are more like those of *S. silone*. The other two pieces are segmented, one being rather dark chestnut brown and more rigid.

The diameter of the two lighter tubes is 0.16–0.17 mm and the darker, sturdier one measures 0.18–0.19 mm across. The rings are very thin toward the ends of the tube (about 9  $\mu$ ), gradually becoming about 18–19  $\mu$ , and then, where the rings double, they measure about 36–40  $\mu$  long, or about  $\frac{1}{4}$  the diameter

of the tube. There are from 16–24 rings per segment.

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# New Records and Observations on the Flapjack Devilfish, *Opisthoteuthis californiana* Berry<sup>1</sup>

WALTER T. PEREYRA<sup>2</sup>

IN JUNE 1961 the U. S. Bureau of Commercial Fisheries joined with the Atomic Energy Commission to undertake an investigation of the deep-water ocean fauna in the area contiguous to the Columbia River mouth at depths from 50 to 1050 fathoms (91–1920 m). The main objectives of this project are to describe the benthic fish and invertebrate communities inhabiting the study area, and to define their bathymetric distribution on a temporal basis. Associated with the faunal investigation is a monitoring of the various demersal forms to evaluate the biological transport of radionuclides which may have their origin in Columbia River waters.

Thirty-one specimens of the flapjack devilfish, *Opisthoteuthis californiana*, have been captured since initiation of the field program in 1961. Records of these captures, together with records of this species from other areas in the northeastern Pacific, are used here to describe the bathymetric and geographic distribution of *O. californiana* and to augment knowledge of its biology.

The flapjack devilfish was described and named by Berry in 1949 from two mature females captured in 188 fathoms (344 m) by a commercial trawler off Humboldt Bay, California. A second paper by Berry (1952) illustrates and gives additional descriptions of these specimens. A male and a juvenile female flapjack devilfish were taken two years later in 280 fathoms (512 m) off Humboldt County, California, also by a commercial trawler. The male specimen was described in detail, especially with

respect to the development of secondary sexual characteristics (Berry, 1954 and 1955). The four specimens reported by Berry (two mature females, one mature male, and a juvenile female) represent the only previous records of this species known to the author.

Throughout the world, six other species of this genus have been described. Two species are known from the Atlantic (the genus type *O. agassizii* Verrill, 1883 and an apparent pelagic species, *O. medusoides* Thiele, 1915), one from the Indian ocean off the west coast of Sumatra (*O. extensa* Thiele, 1915), two from Australian waters (*O. persephone* Berry, 1918 and *O. pluto* Berry, 1918), and one which has been taken repeatedly in Japanese waters (*O. depressa* Ijima and Ikeda, 1895).

Despite wide interest in the taxonomy and comparative morphology of this divergent cephalopod group (Robson, 1925 and 1929), very little is known of their feeding habits, mode of life, or behavior. As late as 1952 Berry (p. 187) wrote of his hope "... that we may not have long to wait before further examples of so strange and interesting an animal will be captured and that something may then be learned of its appearance in the living state, its behavior and habits."

## ACKNOWLEDGMENTS

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<sup>2</sup> Fishery Biologist, Exploratory Fishing and Gear Research Base, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, Seattle, Washington.

TABLE 1  
COLLECTION DATA FOR THIRTY-NINE *Opisthoteuthis californiana*  
TAKEN IN THE NORTHEASTERN PACIFIC

DATE	POSITION		DEPTH (fathoms)	TEMP. (°C)		BOT. SAL. ‰	NO.	SEX	SIZE (mm.)	REMARKS
	Lat. N	Long. W		Surf.	Bot.					
SW of Columbia River off Oregon										
1 July 1961	46° 05'	124° 49.0'	300-303	16.1	...	...	1	undetermined	undetermined	
3 July 1961	45° 51.8'	124° 48.5'	425	16.9	...	...	1	mat. F	225 × 250	
3 July 1961	45° 50.3'	124° 50.0'	450-500	16.3	...	...	1	immat. F	180 × 200	
16 Sept. 1961	45° 56.3'	124° 47.8'	372-374	16.1	...	...	1	mat. M	460 × 440	
10 Dec. 1961	45° 58.5'	124° 49.1'	350	10.0	...	...	1	mat. F	225 × 224	
10 Dec. 1961	45° 52.2'	124° 53.7'	455-475	10.0	...	...	1	undetermined	undetermined	
11 Dec. 1961	45° 58.4'	124° 49.6'	335	9.9	...	...	1	mat. M	195 × 175	Wt. 2 lb
11 Dec. 1961	45° 55.9'	124° 48.1'	372-380	10.0	...	...	1	mat. M	280 × 260	
							1	mat. M	340 × 330	
							1	mat. M	280 × 260	
							1	mat. M	420 × 380	
							1	mat. M	205 × 200	
6 Mar. 1962	45° 52.4'	124° 49.7'	446-455	9.2	4.6	34.192	1	immat. F	170 × 180	Wt. 1.5 lb
7 Mar. 1962	45° 58.5'	124° 52.1'	415-427	8.3	4.6	34.137	1	mat. F	210 × 150	Wt. 1.5 lb
							1	immat. F	190 × 180	Wt. 1.5 lb
11 Mar. 1962	45° 55.5'	124° 46.1'	318-333	7.8	5.8	34.021	1	immat. M	145 × 140	Wt. 1 lb
26 May 1962	45° 58.8'	124° 50.6'	350	13.3	...	...	1	mat. M	440 × 420	
27 May 1962	45° 58.1'	124° 51.5'	375	12.2	...	...	1	mat. M	290 × 290	
27 May 1962	45° 59.3'	124° 52.2'	400	12.8	...	...	1	mat. F	205 × 205	
27 May 1962	45° 54.1'	124° 54.5'	450	13.3	...	...	1	mat. F	210 × 205	
30 Aug. 1962	45° 58.0'	124° 44.7'	250	16.7	...	...	1	mat. M	250 × 240	
31 Aug. 1962	45° 55.6'	124° 46.2'	350	16.7	...	...	1	mat. M	285 × 260	
							1	mat. M	200 × 220	
1 Sept. 1962	45° 54.0'	124° 47.2'	375	16.7	...	...	1	undetermined	small	
23 Jan. 1963	45° 50.9'	124° 52.8'	440-450	8.3	4.7	34.13	1	immat. M	140 × 125	
							1	mat. M	360 × 350	
23 Jan. 1963	45° 54.2'	124° 53.8'	405	8.3	5.1	34.09	1	mat. M	145 × 128	
24 Jan. 1963	45° 55.0'	124° 47.4'	348-354	8.9	4.6	34.18	1	immat. M	260 × 230	
9 May 1963	46° 00.1'	124° 50.8'	300	11.7	...	...	1	mat. M		
13 May 1963	45° 55.8'	124° 49.8'	375	12.2	...	...	1	mat. M		
13 May 1963	45° 52.3'	124° 52.0'	450	12.2	...	...	1	mat. M	310 × 300	
							1	mat. M	360 × 340	

Off Washington									
25 Sept. 1952	47° 29.3'	125° 11.0'	304-308	...	...	1	undetermined	Taken in off-bottom trawl approx. 3 fath. off bottom	
14 May 1963	47° 57.7'	125° 35.5'	150	11.6	5.0	1	F		
Gulf of Alaska									
14 May 1961	53° 38.0'	165° 00.0'	230	...	...	1	mat. M	350 × 340	S of Unimak I.
4 May 1962	57° 29.0'	150° 09.5'	250-256	5.8	5.0	1	mat. M	240 × 230	E of Kodiak I.
6 Apr. 1962	54° 21.0'	159° 45.0'	300	...	...	2	mat. M	large	
17 Sept. 1962	59° 34.0'	145° 45.0'	118	...	...	1	mat. M	415 × 400	WSW Cape St. Elias
17 Sept. 1962	59° 33.0'	145° 17.0'	68	...	...	1	mat. F	285 × 275	WSW Cape St. Elias

Rehder is greatly appreciated. Special thanks are due Dr. Grace Pickford, Bingham Oceanographic Laboratory, Yale University, and Mr. Clifford Fiscus for critical review of the manuscript.

METHODS AND MATERIALS

All the specimens agreed with Berry's description of *Opisthotenthis californiana*, but no comparison was made with species types. Specimens were compared with representatives of two closely related species, *O. depressa* and *Staurotenthis albatrossi*.

The majority of specimens reported in this paper were taken along a trackline running southwest from the Columbia River mouth. On this trackline standard stations were established at depths ranging from 50 to 1050 fathoms (91-1920 m). These stations were monitored four times a year, principally with a 400-mesh Eastern otter trawl, a 43-ft Gulf of Mexico shrimp trawl, and a 70-ft semi-balloon shrimp trawl. The latter two trawls were used when trawling at depths greater than 450 fathoms (823 m). Vessels used to survey the trackline were the M/V "Commando," a 65-ft purse-seine type vessel chartered from the College of Fisheries, University of Washington; and the M/V "John N. Cobb," the Bureau's 93-ft exploratory fishing vessel.

Observations on 39 flapjack devilfish collected in the northeast Pacific are reported in this paper (Table 1). Of this total, 31 specimens were taken on the Columbia River trackline by the M/V "Commando" and "John N. Cobb," two off the coast of Washington by the "Cobb," and six in the Gulf of Alaska by the "Cobb" and chartered vessels of the International Pacific Halibut Commission. All specimens were captured with the 400-mesh otter trawl, with the exception of one taken on the Washington coast in a large pelagic trawl rigged to fish just off-bottom. None of the sampling gear used was a closing net. Therefore, although all of these captures, with one exception, are treated as occurring on the bottom, the possibility exists that they could have been taken as the gear was being set or hauled back.



Observations on living animals were made in a 20-gallon aquarium with a sealed top aboard the M/V "John N. Cobb" during a cruise in January 1962. Motion pictures were taken at this time which allowed a more detailed behavioral analysis to be made on shore.

#### OBSERVATIONS

##### *Geographic Distribution*

Prior to this study the known geographic distribution of *O. californiana* was recorded from four specimens reported by Berry (1949: 24; 1952:183; 1954:29; and 1955:219, 223). The exact locations for these captures are not given, but from Berry's descriptions they apparently were confined to a small area off Humboldt Bay, California (approximately 45°10'N, 125°10'W).

The data in Table 1 extend the geographic range northward 2200 miles along the continental shelf to off Unimak Island, Alaska—that is, from northern California to the Aleutian Islands, Alaska.

##### *Bathymetric and Seasonal Distribution*

The known bathymetric range of this species off northern California as recorded by Berry (ibid.) is from 188 to 280 fathoms (344–512 m). Specimens collected from the Columbia River trackline were taken at depths from 250 to 450 fathoms (457–823 m); those off Washington from 150 and 308 fathoms (274–563 m); and those from the Gulf of Alaska from 68 to 300 fathoms (124–548 m). The above records extend the known bathymetric range shoreward to 68 fathoms (124 m) and seaward to a depth of 450 fathoms (823 m). As has been observed for the western Pacific congener (*O. depressa*), *O. californiana* has been collected from shallower water at the northern end of its range, with the bathymetric range being wider to the north despite infrequent trawling in water deeper than 300 fathoms in northern waters.

The known bathymetric ranges of the other species of *Opisthotentis* are not all similar (Robson, 1929:167–173). Both *O. depressa* from Japanese waters and *O. agassizii* from the North Atlantic have been reported at greater

depths (587 and 1058 fathoms [1073 and 1934 m], respectively) than *O. californiana*. The bathymetric ranges of the other four species, *O. extensa*, *persephone*, *pluto*, and *medusoides*, fall within that of *O. californiana*.

The temporal distribution of males and females by depth along the Columbia River trackline is presented in Figure 1. Although the number of specimens is small, males appear to occupy a greater bathymetric range than females. The latter were never captured at depths shallower than 375 fathoms (686 m). There are, however, three known records of females from levels shallower than 375 fathoms (686 m): one off California in 188 fathoms (344 m) (Berry, 1949:24), one off Washington in 150 fathoms (274 m), and one from the Gulf of Alaska in 68 fathoms (124 m).

On the trackline the data suggest that the males may move seasonally, being found at shallower depths in the summer. Perhaps mating takes place in late winter when the sexes occupy similar depth zones, but this is only a surmise.

In cephalopods a separation of the sexes by depth has been noted by several authors. Isgrove (1909:472) notes a disparity in the sex ratio of *Eledone*. She suggests that the disparity is caused by the females breeding in littoral waters, in which they are more frequently taken. Robson (1925:1325) presents figures for Octopodidae picked at random from selected reports, where inside of 200 fathoms (366 m) the percentage of females is greater and outside the percentage of males is greater. Both of the above findings, where the female Octopodidae predominate in shallow water, are reversals of the situation which has been found in this study for *Opisthotentis*, where the males predominate in shallow water.

Of the specimens collected off the north Oregon coast for which the sex is known, 18 males and 10 females are recorded. Since greater trawling effort was expended at the depths where the males predominate (in the shallow part of the range), the above ratio probably does not reflect the actual sex ratio.

##### *Availability*

Catch-per-hour trawling for *O. californiana* at various depths is given in Figure 2. The data

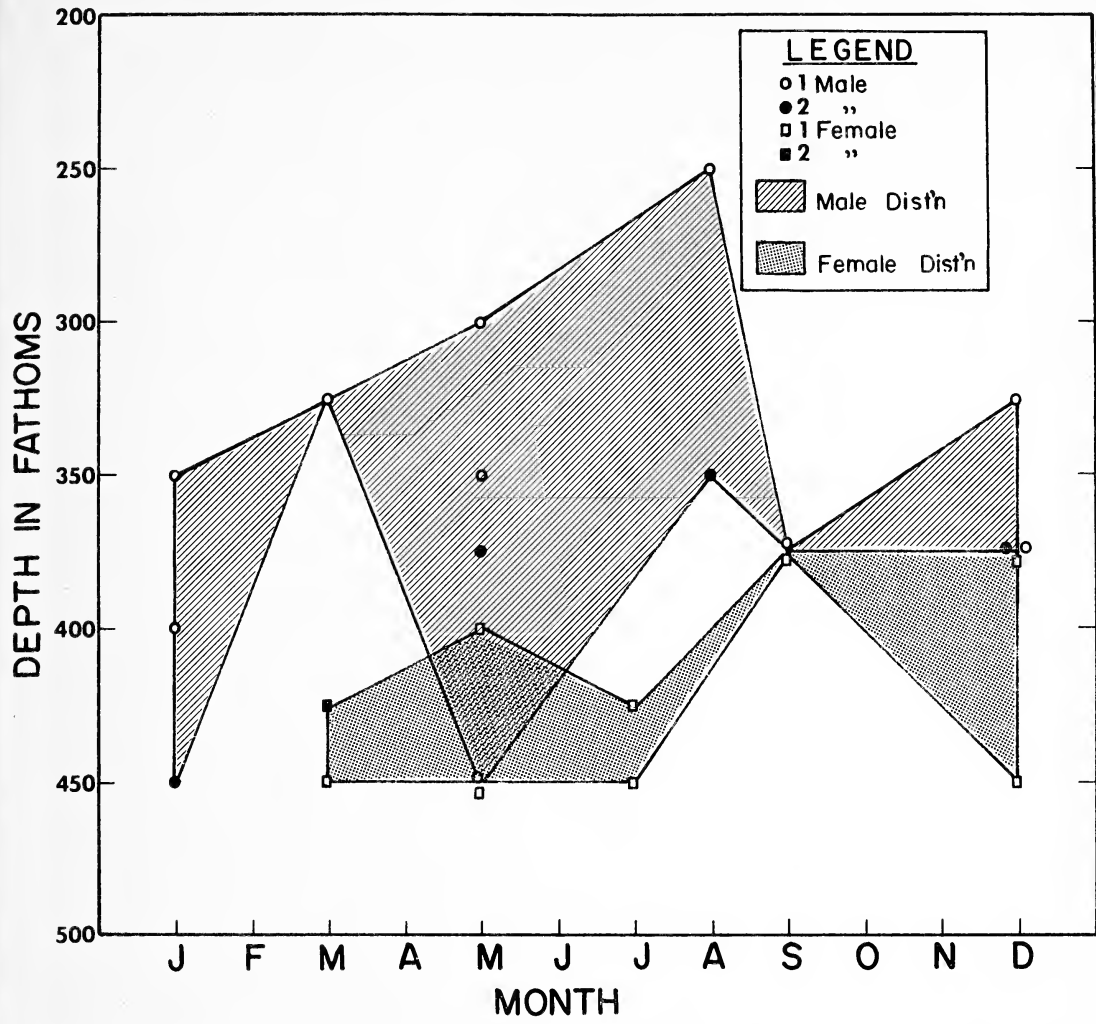


FIG. 1. Temporal and bathymetric distribution of male and female *Opisthoteuthis californiana* based on capture of 28 individuals on a trackline off the mouth of the Columbia River, July 1961–May 1963.

suggest that Berry (1949:26 and 1952:183) was correct in surmising that these animals are probably not unduly rare where suitable bottom conditions exist. The average catch rate over the depth range where they were taken on the Columbia River trackline was approximately 0.4 individuals per hour of trawling (Table 2). Within the range of depth where the species were found, they were most frequently encountered from 375 to 450 fathoms (686–823 m). Due to the low effort from 475 to 575 fathoms (868–1051 m), where only two drags have been made, its relative abundance in deeper water is not well known.

The bimodal nature of the catch-per-unit-of-effort curve may result from several factors. As shown earlier, the sexes are distributed unevenly, with the males found in shallower water than the females. This could create the apparent non-normal distribution. Another factor which may be responsible is the direct or indirect effect of bottom type on distribution. Green mud was found to predominate over the range where the species was encountered; but inside of 325 fathoms (594 m) and at 400 fathoms (731 m), where the catch per effort was low, the sand/mud ratio was higher ( $> .08$ ) than was found at adjacent stations

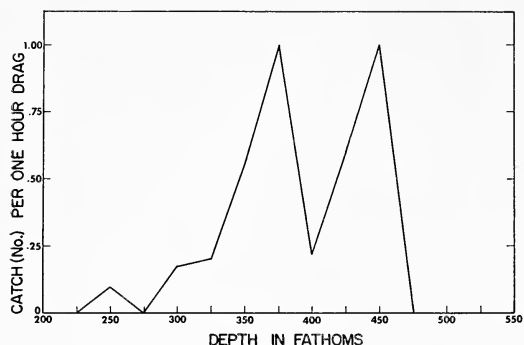


FIG. 2. Number of *Opisthoteuthis californiana* caught per one-hour of trawling by 25-fathom depth intervals from the Columbia River trackline.

(Dr. Dean McManus, unpublished data). Additionally, at 275 fathoms (503 m), where no specimens were captured, outcroppings were encountered. The above findings are presented as possible explanations, not conclusions.

### Morphology

The external appearance of animals of this genus is quite peculiar. General descriptions in the past have invariably been made on preserved specimens or on specimens which were not alive in water; consequently the common name, flapjack devilfish, has arisen in the literature. Berry (1952:183) goes so far as to state that in the preserved state these animals resemble in about equal degree a soggy pancake or a very dirty floor mop. The lack of supporting structures, webbing between the arms, and the extent of gelatinous tissue makes this description true. But when the animal is observed alive in water, a different picture is presented (Fig. 3).

With the mantle cavity and gelatinous tissues supported by water the shape, as viewed anteriorly, appears more like a wide bell than the plano-convex disc used to describe preserved material. Viewed from the side the anterior portion of the head and body proper slope gradually dorsad, with the dorsal surface being rather flattened. The posterior margin slopes very abruptly, almost perpendicularly, away from the dorsal surface. Thus, the cephalic mass is considerably expanded and raised, being displaced posteriorly.

The eye openings are not large and the

rounded eye prominences, which are noticeable on the upper surface of preserved material, disappear when the animal assumes a normal shape. Conversely, the ear-like fins become more noticeable on live specimens.

When the animal is at rest (Fig. 3a), there is a horizontal curvature of the distal portion of the arms anteriorly, a condition similar to that described for preserved specimens (Ijima and Ikeda, 1895:329). The lateral curving of the right and left arms anteriorly results in the dorsal or anterior arms facing each other with their concavity while the ventral or posterior arms face with their convexity. The ends of the latter pair of arms are, therefore, turned laterally away from each other.

When at rest in an aquarium, the oral surface did not lie flat to the bottom, as might be expected. Instead, the distal half of the animal was held off the bottom (an inch or so in larger specimens) with only the basal portions of the arms in contact with the bottom (Fig. 3b). Interestingly, this area of contact on the arms is the portion possessing the largest suckers (excepting the 6-7 enlarged suckers distally on the dorsal pair of arms on the males, which have a specialized function [Berry, 1955: 221]). Yet, at no time were the animals observed to hold with these or other suckers. As

TABLE 2

NUMBER OF *Opisthoteuthis californiana* CAUGHT PER ONE-HOUR DRAG WITH A 400-MESH COMMERCIAL OTTER TRAWL BY 25 FATHOM DEPTH INTERVALS ON A TRACKLINE OFF THE MOUTH OF THE COLUMBIA RIVER.\*

DEPTH (fathoms)	NO. SPECIMENS (C)	NO. DRAGS (f)	C/f
250	1	11	0.09
275	0	8	0
300	2	12	0.17
325	2	10	0.20
350	5	9	0.56
375	9	9	1.00
400	2	9	0.22
425	3	5	0.60
450	7	7	1.00
Σ	31	80	

\* Only drags at depths where captures have been made in this area are included.

$C/f = 31/80 = 0.388$ .

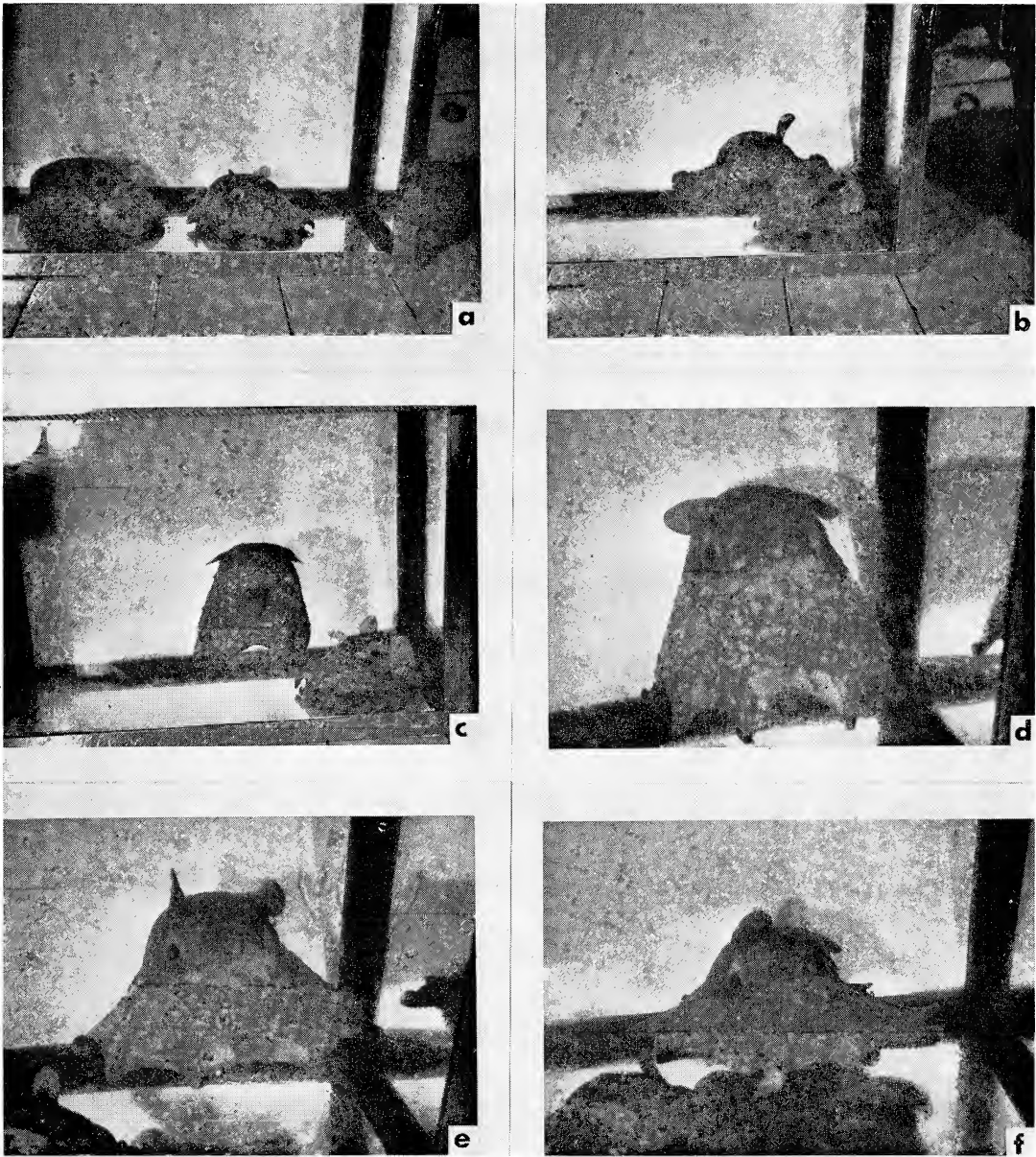


FIG. 3. Behavior of live *Opisthoteuthis californiana* in an aquarium. *a-d*, swimming off bottom; *e-f*, setting back to bottom.

the vessel rolled, flapjack devilfish moved back and forth in the aquarium. A small *Octopus* sp., placed in the aquarium at the same time, had no trouble "hanging on" or clinging to the aquarium. The inability of the flapjack devilfish to attach to the aquarium glass, even though the males possess many greatly enlarged suckers, sheds more light on the degeneracy of this

cephalopod group and allows questions as to the function of these enlarged suckers. Assuming that these animals behaved normally despite the fact that they had been brought to the surface, it would not seem that this cephalopod can apply itself to a rock as stated by Borradaile et al. (1935:602), or attach to a projecting substratum as stated by Ijima and Ikeda (1895:

328), or is a creeping or clinging form as Verrill (1896:74) thought.

The highly specialized dorsal arm-pair of the males, regarded as the hectocotylized or nuptial arms, with their 6-7 greatly enlarged globular suckers distally, is characteristic of this species (Berry, 1955:221-222). This condition, of course, reaches its highest degree of development in the mature males; but even with the smaller immature males, three of which are present in this series, the distal suckers of the dorsal arm-pair are slightly enlarged. The sexes are, therefore, always distinguishable by this male nuptial arm character.

The internal structuring of this group is more striking than the external. Many organs are completely lost with no new structures replacing them. There are no salivary glands, no ink sac, no well defined crop, no radula, and no right oviduct (Berry, 1952:185). The stomach is quite small, and is divided into two parts; the liver is bilobed. The reproductive apparatus of both sexes is massive, and in mature individuals it constitutes a considerable portion of the visceral mass (Figs. 4 and 5).

#### Color

In life the coloration differed slightly from that reported by Berry (1949:24 and 1952:186) for preserved material ("... light dull drab, very heavily concentrically streaked with dull dark reddish brown . . ."), being a more evenly distributed dark reddish brown with breaks of light blue in the background coloration.

There was no concentric streaking as Berry observed for preserved material, and no aboral spotting as is reported for several congeners (Berry, 1918:286, 291; Sasaki, 1929:11; and Verrill, 1883:114). The oral surface was likewise dark reddish brown but without the breaks in the background coloration. This dark reddish brown coloration diffuses to a pale reddish tan color in the region of the cirri, suckers, and the central portion of the arms. After preservation the coloration was similar to that reported by Berry (1952:186).

The light blue breaks in the reddish brown coloration were due to splitting of the delicate outer skin of the aboral surface by trawl abrasion and from the spines of fish in the catch. This point was verified by purposely splitting the outer skin of freshly caught specimens. The light blue coloration became evident immediately. The degree of skin splitting varied with the individual, some being so badly abraded that the brown coloration was almost completely wanting.

#### Fecundity

Egg counts and measurements were made on three mature females captured at different times of the year. These data are presented in Table 3.

The total egg count varied from 225 to 475 eggs. In none of the individuals examined was the egg size uniform; it varied from less than one mm to 11 mm in greatest diameter (length). The largest egg examined measured 11 by 6 mm, which is slightly larger than the largest

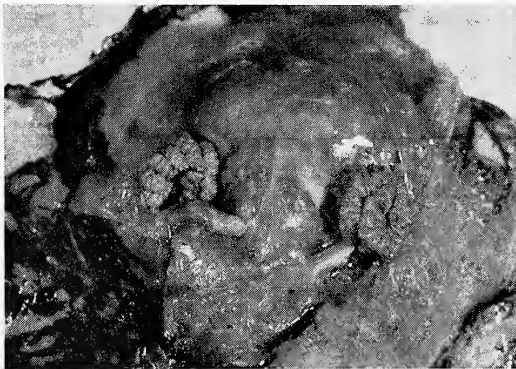


FIG. 4. Reproductive organs of a mature female *Opisthoteuthis californiana*,  $\times .45$ .



FIG. 5. Reproductive organs of a mature male *Opisthoteuthis californiana*,  $\times .65$ .

TABLE 3  
FECUNDITY OBSERVATIONS ON THREE MATURE FEMALE *Opisthoteuthis californiana*  
TAKEN ON THE COLUMBIA RIVER TRACKLINE

DATE	DEPTH (fathoms)	SIZE (mm)	TOTAL VOLUME EGGS (ml)	NO. EGGS ≥3 mm (length)	NO. EGGS <3 mm (length)	% LARGE EGGS	LARGEST EGG (mm) LENGTH × WIDTH
3-7-62	425	210 × 150	5.0	98	150-200	33-39	10 × 5
7-3-61	425	255 × 250	3.3	125	150-200	46-56	9 × 5
12-11-61	375	340 × 330	23.0	324	125-150	68-72	11 × 6

egg reported by Berry (1952:185) (9 by 5 mm). The percentage of large eggs (greater than or less than 3 mm in length was arbitrarily chosen to designate large and small eggs, respectively) differed for each individual, with a range from 33 to 72%. Likewise, the volume of eggs in the ovary ranged from 3.3 ml to 23.0 ml. In the specimen with 72% large eggs (egg volume of 23.0 ml), the majority of the large eggs were located in the upper part of the ovary with ripe eggs spirally arranged in a compact group just under the oviducal gland (Fig. 4). In no case was there any indication of stalk development.

The extent of egg development was used as circumstantial evidence indicating the season of ovulation. The highest degree of egg development was observed in a female containing ripe eggs, captured on the 11th of December. The least development was found for the March capture, while the female captured in July showed an intermediate degree of development. With only three samples represented no unequivocal conclusions are permitted, but indications are that ovulation occurs during the winter.

Food

The stomachs of eight specimens were examined to ascertain the food organisms (Table 4). Only one stomach was found completely empty and the remaining stomachs contained very little, never more than 5 ml. The material in greatest abundance was crustacean remains, mostly small mysids (approximately 7 mm in length) and large copepods. Only one non-crustacean organism was found, a polychaete; and this was partially digested and positive

identification was not possible. A few amphipods, isopods, and a masticated shrimp, probably a hippolytid or crangonid species, were also recognized. No quantities of mud were mixed in with the stomach contents, but a few sand grains were found in the stomach of the Unimak Island specimen. In some stomachs a brown organic material was found mixed with the food, but the exact composition of this material is not known. Fecal remains left in the aquarium by the live individual appeared to contain this same material.

The above summary of gut-contents partially substantiates the speculation by Berry (1952:187) that this species feeds mainly on micro-plankton or detritus swept down the disc by the radial series of cirri toward the mouth. The detrital element of its diet has not been substantiated, but the presence of the small crustaceans in the gut verified the planktonic feeding habit. The size of the plankton indicates that the animal is more of a macro- than a micro-plankton feeder.

A few mysids found in the esophagus of one individual were entire, as were most of those found in the first stomach of the others. Only one organism was noticeably bitten, the small hippolytid or crangonid shrimp. Thus it appears that except for a few of the larger organisms the majority were taken entire and not first reduced by the strong beak. As Robson (1925:1348-1349) has suggested, the food is probably ground down in the muscular first stomach and digested in the second, instead of being partially comminuted by the radula with preliminary digestion in the crop, as occurs in species that possess the latter two structures.



### Locomotion

Observations made on live individuals in an aquarium revealed a most interesting locomotory pattern. Although most octopods, with the exception of the pelagic species such as *Cirroteuthis*, move about principally by two methods, "crawling" and rapid ejection of water from the siphon, the flapjack devilfish, owing to its unusual anatomical features, is not able to move effectively by these means. The very weak suckers and the loss of free arm movement due to webbing prevent crawling; and the reduction in the mantle aperture consequent to the posterior placement of the siphon greatly decreases the effectiveness of the siphon as a locomotory organ.

The principal means of progression, as observed in the aquarium, was by opening and closing of the webbed "umbrella" together with fin movement. The general pattern of this method of locomotion, which was analogous to that of a jellyfish, is seen in Figure 3 *a-f*.

From a resting state the animal initiated movement by extreme opening of the umbrella (Fig. 3*b*). This caused the oral surface to take on a convex shape with the arms curved slightly upwards and anteriorly. Following this, the umbrella was closed by a

powerful downward stroke, which reduced the opening into the concavity of the now closed umbrella to about one-half the diameter of the animal (Fig. 3*c*). This action forced the animal off the bottom by (1) the actual contact of the downward thrusting arms with the bottom and (2) the interaction of the closing oral surface with the water. This pattern of opening and closing the umbrella was repeated so that the animal remained off the bottom. The closing action was about twice as rapid as the opening. With each stroke the devilfish would move from 4 to 12 inches depending on the thrust of the closing stroke, and the tempo and direction of movement. The swimming motion was observed to progress as rapidly as one stroke every two seconds, although the usual tempo was once every four seconds. With movement at the higher rate the animal was carried to the surface of the aquarium in three to four strokes. Subsequent to termination of swimming, the animal opened its umbrella into the convex shape, thereby descending slowly (Fig. 3*f*). When swimming the animal occasionally made partial strokes instead of complete ones.

With contraction of the umbrella a jet of water was ejected from the siphon (Fig. 3*c*). This jet could be directed by the siphon left

TABLE 4

STOMACH CONTENTS OF EIGHT *Opisthotenthis californiana* COLLECTED IN THE NORTHEAST PACIFIC

DATE	DEPTH (fathoms)	LOCATION	ANIMAL SIZE (mm)	STOMACH VOL. (ml)	CONTENTS
5-14-61	425	Gulf of Alaska	350 × 340	<1	crustacean remains including 1 amphipod; some sand grains
7-3-61	425	off north Oregon coast	255 × 250	<1	nothing which could be made out
12-11-61	335	off north Oregon coast	420 × 380	....	empty
12-11-61	375	off north Oregon coast	280 × 260	2	crustacean remains; 3 mysids approx. 7 mm long
12-11-61	375	off north Oregon coast	340 × 330	4	8 mysids, largest 10 mm; 4 amphipods, 9 copepods, 2 isopods, 1 crangonid or hippolytid shrimp approx. 22 mm
3-7-62	425	off north Oregon coast	190 × 180	1	crustacean remains, mostly copepods
3-7-62	425	off north Oregon coast	210 × 150	3	same as above plus partly digested polychaete?
8-30-62	250	off north Oregon coast	250 × 240	1	crustacean remains, mostly copepods

or right, to the posterior, or down. But because the ejection was feeble, it added only slightly to the net movement. Verrill (1896:74) and Berry (1952:184) were correct in stating that the siphon appeared to be too small to be used for efficient locomotion.

The two dorsal fins, which heretofore had been considered as "inefficient looking" (Berry, 1952:183), moved in a highly coordinated manner, augmenting the effect of the umbrella movement. (This is consistent with their morphology, inasmuch as they are supported by a cartilaginous rod and possess ample musculature.) Balancing and orientation of the animal were the main functions of the fins, but during certain phases of swimming they appeared to assist locomotion.

When at rest the fins were positioned at the side of the head just behind the eyes in a down position, with the free-edge which contained the cartilaginous rod posterior (Fig. 3*a* left). The fins could point slightly posteriorly but never anteriorly.

Fin movement began with an up-stroke (Fig. 3*a* right). The supported posterior edge led on this stroke, resulting in the fin moving through the water with the least resistance (Fig. 3*d*). This stroke was terminated after the fin had moved upward almost 180° (Fig. 3*e*). On the down-stroke the supported posterior edge again moved the fin, but this time the transverse axis was perpendicular to the direction of fin movement, offering the greatest surface area to come in contact with the water (Fig. 3*c*). Because of this, fin movement on the up-stroke was faster than on the down-stroke. This pattern of least resistance on the up-stroke and greatest on the down-stroke created an upward resultant force. Both fins were usually moved together in the same direction, but occasionally they were moved alternately, or one might be moved while the other was not. (Fig. 3*b*, *f*).

Although the basic fin movement was always the same, the axis of movement could be shifted 90° forward from the up-down to an anterior-posterior direction or to any degree between these extremes. The greatest surface area of the fin was exposed on the posterior or down-stroke. This permitted net movement in any direction from upward to forward or anterior.

Thus, by moving the fins alternately or together, and by adjusting the axis of movement and the strength of the stroke, the animal had considerable control over the direction of movement created by the powerful undulations of the umbrella. The animal might swim up, sideways, or down depending on its attitude at the time of the umbrella closing.

The tempo of fin movement was always greater than that of umbrella movement. Usually it was in the ratio of three fin strokes to every umbrella stroke, but this varied. Also, the fin movement was coordinated so that a down-stroke coincided with the closing of the umbrella.

When the animal was at rest on the bottom, fin movement usually continued, but at a slower rate and in various directions. Also, the pattern of fin movement was generally alternate.

As the swimming undulations of the umbrella ceased and the animal settled to the bottom, the tempo of fin movement increased considerably in an alternate pattern. This increased fin activity probably helped to slow the animal's descent and provided for better attitude control.

The alternate fin movement pattern was surprising. Considering that both fins are supported by a common cartilaginous rod, this rod must be able to undergo considerable torsion for the fins to be moved alternately.

The use of photofloods to take pictures revealed a negative light reaction. Prior to turning on the photofloods, the animals actively moved in the aquarium under subdued light. When the photofloods were turned on, activity continued for 15 to 20 seconds and then all movement ceased. As long as the photofloods were on, the animal remained perfectly still.

Several authors have hinted at the existence of the pulsating locomotory pattern from knowledge of the gross morphology of the species. Ijima and Ikeda (1895:328) stated "... that alternate closure and expansion of the arms is of much greater moment to *Opisthoteuthis* than to most other Cephalopods, since the ejection of water from the comparatively small branchial chamber and siphon must be of subordinate significance." Berry (1952:184) offered similar speculations, stating that the



undulations or opening and closing of the arms might be quite significant. Robson (1929:22, 28) also stated that the web is probably used in locomotion. He commented that the web becomes deep independently in the Cirromorpha and the abyssal Octopodidae and that this convergent resemblance is suggestive of some identity of adaptation.

Verrill (1896:74-75), by deducing function from structure, put forth several possibilities as to means of movement for members of this group that conflict with the above opinions. He felt that *Opisthotenthis* was a crawling or creeping form, having concluded that the union of the eight arms with the web formed a disc-like ventral foot, and therefore, was analogous to that of a chiton or limpet. The small lateral fins indicated to him that *Opisthotenthis* could swim, more or less, and that undulatory movements of the lateral edge of the pedal disc might be possible. But he felt that a pulsating swimming motion by the umbrella, similar to that of *Cirrotenuthis*, would not be possible because adhesion of the arms and web to the body would prevent their free use. It can be seen that, by approaching function in this manner, his deductive reasoning was, for the most part, erroneous.

Certain Octopodidae have also been observed to swim by opening and closing the web. Verrill (1882:373) states that *Bathypolypus arcticus* swims in this manner, as does *Eledone moschata*, according to Orbigny and Ferussac (1840). Wells (1962:3) comments that *Cirrothauuma* employs a jellyfish-like locomotion. Another species of *Eledone*, *E. cirrosa*, uses its web only when sinking downwards (Isgrove, 1909: 472-473).

The main function of the swimming pattern could be to facilitate travel from one area to the next. This is indicated by the fact that one specimen was apparently captured three fathoms above the bottom in an off-bottom trawl. If bottom currents were strong enough, the animal could travel considerable distances by swimming off the bottom and allowing the currents to carry it passively. Shorter movements could be made by orientation forward together with umbrella pulsations. A combination of these two methods would allow the greatest forward progress.

Another possible function might be food concentration. At times the animals were observed just off the bottom of the aquarium making incomplete swimming motions. Could this possibly represent a method whereby food is concentrated by means of the produced currents? Once the food was concentrated, the animal could settle to the bottom with the umbrella open. This might trap the food organisms under the umbrella and permit feeding.

An escape function is indicated from the reactions of provoked individuals in an aquarium: they moved rapidly upwards when prodded.

### *Habitat*

It is generally felt that members of this group (with the exception of *O. medusoides*) are bottom dwellers. This conclusion has been deduced by several authors through arguments from structure to habitat (Berry, 1952:184; Dollo, 1912; and Meyer, 1906). The pigmentation, depressed form, dorsal eyes, and general body shape all are indicative of a benthic existence. Observations and data from this paper are further supporting evidence for a benthic existence.

Even though numerous drags along the Columbia River trackline have been made shallower and deeper than the known bathymetric range of this species, the captures of flapjack devilfish are restricted to the interval from 250 to 450 fathoms (457-823 m). This indicates that the species is benthic; for if it were pelagic, and if the trawl captured these animals while being set or hauled, we would expect to have captures over a wider depth range. The one off-bottom capture, which might be argued as being pelagic, should still be classed as a bottom capture, because of its proximity to the bottom.

Extensive midwater trawling off central and northern Oregon by Oregon State University personnel has not produced a single flapjack devilfish (Dr. William Percy, written communication). This is further supporting evidence of a non-pelagic existence.

Observational data further support a benthic existence. The negative buoyancy, together with the manner in which the animal swims off the

bottom and settles down again, are supporting evidence.

Although the animal is primarily a bottom dweller, it is doubtful that it burrows in the mud. The locomotory behavior of specimens in an aquarium, the capture of one specimen just off the bottom, and the lack of mud and infauna in the gut imply epibenthic existence. Although most of the food organisms recovered from the gut were not epi- or infauna, indicating a truly benthic feeding habit, none appeared morphologically to be pelagic.

Hydrographic data have been taken coincident with some of the captures of *O. californiana*. Bottom water temperature ranged from 4.6 to 5.8° C, and salinity was approximately 34.1 ‰, and bottom type consisted primarily of greenish silt, occasionally mixed with small amounts of sand and clay. Since this bottom type is associated with a smooth bottom which is, therefore, more conducive to trawling, flapjack devilfish may inhabit rocky areas which have not as yet been sampled.

Authors in the past have classified *Opisthotentis* as an abyssal animal (Dollo, 1912 and Meyer, 1906). According to Hedgpeth (1957: 21) the limits of the abyssal region are from 2000 or 3000 m (1092–1622 fathoms) downward to about 6000 m (3241 fathoms). The upper limit may better be defined as the region in which the temperature never exceeds 4° C. Bruun (1957:643) remarks that in the Atlantic Ocean this temperature is not reached until about 2000 m (1082 fathoms), whereas in the Indian and Pacific oceans it is as high as 1500 or 1000 m (811 or 541 fathoms). If we note the upper limit of the abyssal region in the areas of capture, then we must conclude that *Opisthotentis* has not been taken in the abyssal zone. With few exceptions, captures of *Opisthotentis* have been reported from the continental slope. These exceptions were a few specimens of *O. depressa* taken on the continental shelf off Japan at the higher latitudinal limits of this species' range (Sasaki, 1920: 170) where bottom temperatures are lower (Dr. Felix Favorite, personal communication); and one specimen of *O. californiana* captured off Alaska.

### *Evolutionary Considerations*

From what is known of the morphology and habits of *Opisthotentis*, most authors have felt that members of this group are highly evolved, exhibiting numerous degenerate conditions (Berry, 1952; Dollo, 1912; Meyer, 1906; Robson, 1925 and 1929; and Verrill, 1896). The evolutionary significance of some of these conditions is not thoroughly understood and is questioned by Robson (1929).

The following observations are further additions to the concept of specialization and degeneration for *Opisthotentis*: (1) the presence of large suckers which are ineffective for holding on, and (2) a pulsating swimming motion through use of the web, together with highly coordinated fin movement.

The adaptive significance of the deepening of the web convergently in many of the Octopodidae is suggested by the locomotory pattern exhibited by *Opisthotentis* and others (*Bathypolypus arcticus*, *Eledone moschata*, *E. cirrosa*, *Cirrotenuthis*, and *Cirrothauma*). All have an extended web and use it in some phase of swimming. When the behavior patterns of more deep-webbed species are known, we probably will find that the extension of the web is primarily a locomotory adaption.

### SUMMARY

1. Thirty-nine records of the flapjack devilfish, *Opisthotentis californiana*, from off the coasts of Oregon, Washington, and Alaska are reported.

2. The known geographic range of this species is extended from northern California to the Aleutian Islands, Alaska, and the known bathymetric range is now defined from 68 to 450 fathoms (124–823 m).

3. Males occur in shallower water than females, and there is an indication that the males move seasonally, being found in shallower water during the summer. The overall sex ratio appears to be close to 1:1.

4. At the depths of greatest availability (375 and 450 fathoms [686 and 823 m]) off northern Oregon a catch rate of one specimen per one-hour drag was recorded.

5. Observations on living animals revealed that the general appearance was more nearly a bell-shape than a plano-convex disc, with the

eye prominences not noticeable; that at rest there was a horizontal curvature of the distal portion of the arms anteriorly and that the oral surface was not completely in contact with the bottom; that the suckers were ineffective or not used by the animal to hold to the bottom; that contraction and expansion of the umbrella together with coordinated fin movement were the means of movement, with ejection of water from the siphon being of very minor importance; and that the color in life was dark reddish brown with the bluish blotches being the result of rough treatment in the trawl. There was no concentric streaking.

6. Hectocotylization of the dorsal arm-pair can be detected in all males, regardless of maturity.

7. The total egg count of mature females examined ranged from 225 to 475 eggs, with the largest egg found measuring 11 by 6 mm at the greatest diameters. Ovulation was tentatively concluded to occur in the winter.

8. Gut-content analysis showed that these animals feed on small crustacea, mostly large copepods and small mysids. A brown organic substance was found in several stomachs.

9. The benthic existence of this species was further substantiated from catch records and observational data.

the presence of the large ineffective suckers

10. The specialized locomotory behavior and further substantiate the degenerate and specialized nature of *Opisthoteuthis*.

#### ADDENDUM

After the present paper was submitted, Dr. D. B. Quayle, Fisheries Research Board of Canada, Nanaimo, B. C., provided the author with the following two additional records from the northeastern Pacific: (1) Off Unimak Island, Alaska ( $53^{\circ}39'N$ ,  $164^{\circ}44'W$ ) at 238–252 fathoms on August 13, 1964; and (2) off northern Washington ( $47^{\circ}58'N$ ,  $125^{\circ}47'W$ ) at 505–510 fathoms on September 6, 1964. The latter record extends the bathymetric range to 510 fathoms.

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## New Pacific Records of Juvenile Albacore *Thunnus alalunga* (Bonnaterre) from Stomach Contents

HOWARD O. YOSHIDA<sup>1</sup>

BECAUSE THE ALBACORE, *Thunnus alalunga* (Bonnaterre), is commercially one of the more valuable species of tuna, a great deal of effort has been expended in investigating its biology. Although much has been learned in recent years about the albacore, its age and growth, movements and migrations (Otsu, 1960; Clemens, 1961; Otsu and Uchida, 1963), many facets of the biology of this species still need to be studied. As part of the Albacore Ecology Program, staff members of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, have been studying the early life history of albacore in order to fill the gaps in our knowledge.

There is a paucity of information on the juvenile<sup>2</sup> and larval stages of albacore due in part to two factors. One is the limited success of efforts to collect the young, and the other is the difficulty of identifying them, since adult morphological characters are often inadequate for identifying the young stages. Although there has been some success in collecting juvenile tunas with various types of midwater trawls (Matsumoto, 1961), most of the juvenile tunas recorded in the literature have come either from stomachs of predators or from dipnetting at nightlight stations. Yabe, Ueyanagi, Kikawa, and Watanabe (1958) reported on five juvenile albacore less than 30 cm discovered in stomachs of predators caught in the western North and South Pacific Ocean. So far as I know, theirs is the only documented record of juvenile albacore in the Pacific Ocean, and it has positively demonstrated albacore spawning in these areas.

In June 1960, a program was initiated at the Biological Laboratory, Honolulu, to sample

stomachs of large pelagic fishes for juvenile albacore. This paper presents the results of sampling through November 1962. Twelve juveniles were found in stomachs of predators caught in the central North and South Pacific, thereby extending known or demonstrating new spawning grounds for albacore. Although the number of specimens is small, I consider it important to report them promptly since juvenile albacore are not very often collected and the information may be of value to other investigators studying the biology of the albacore.

### SOURCE OF MATERIALS

Two sources of stomach samples that were readily available to the author were the large fishes landed by the Hawaiian commercial longline fishery and by exploratory fishing cruises of the Bureau of Commercial Fisheries' research vessel "Charles H. Gilbert."

The Hawaiian longline fishery is usually conducted within 20 miles of the main islands, with most of the boats in the fleet operating out of Honolulu, while smaller numbers fish out of Hilo and Kona on the island of Hawaii, and from Port Allen on the island of Kauai (Otsu, 1954). The catch of this fishery consists of a variety of large pelagic fishes, including striped marlin (*Makaira audax*), blue marlin (*Makaira ampla*), black marlin (*Istiompax marlina*), broadbill swordfish (*Xipbias gladius*), and shortnose spearfish (*Tetrapturus angustirostris*), among the spearfishes. Among the tunas, bigeye (*Thunnus obesus*), yellowfin (*Thunnus albacares*), and small numbers of albacore and skipjack (*Euthynnus pelamis*) are taken.

Stomachs were sampled at the auction markets of the United Fishing Agency, Ltd., and the Hawaiian Fishing Co., Ltd., in Honolulu. Since it has been shown that juvenile tunas occur more frequently in stomachs of spearfishes

<sup>1</sup> Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received October 1, 1963.

<sup>2</sup> Unless otherwise noted, the term "juvenile" as used herein includes albacore up to 30 cm long.

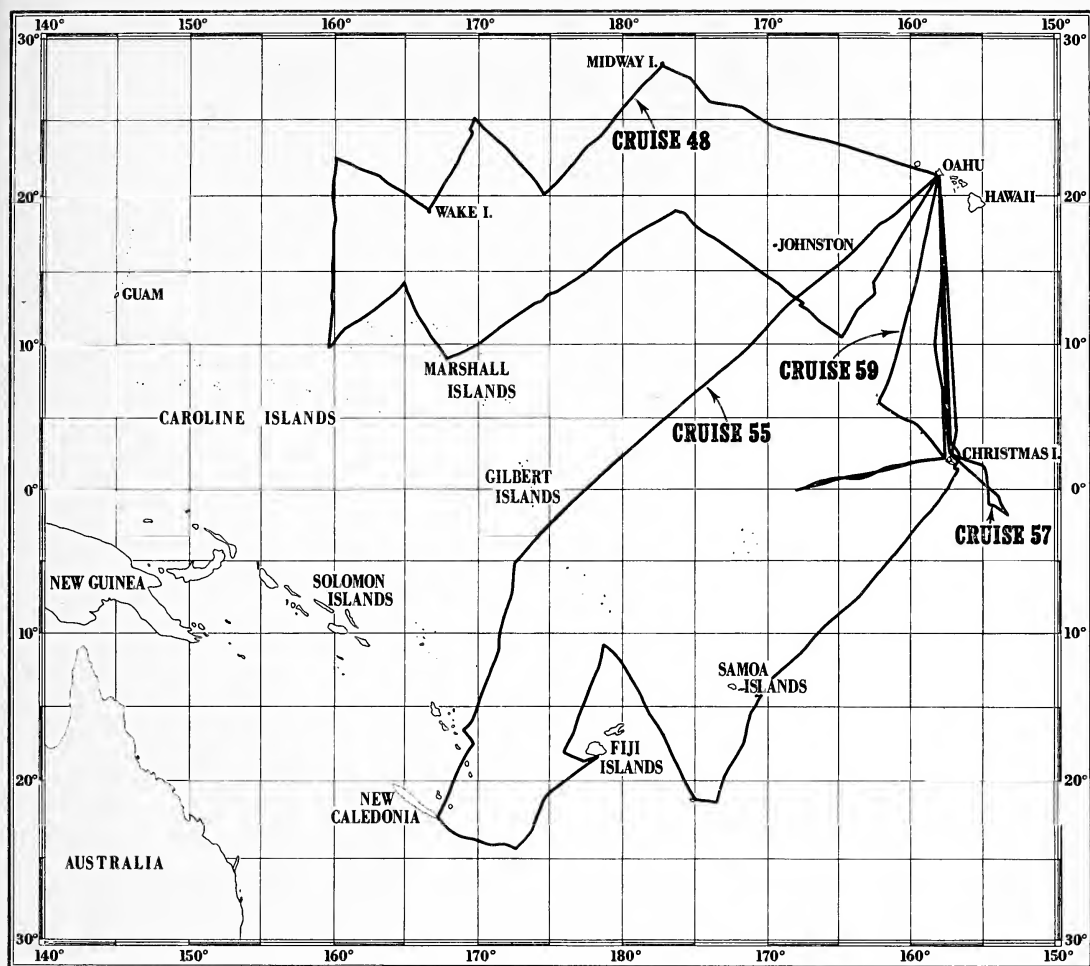


FIG. 1. Tracks of the "Charles H. Gilbert," cruises 48, 55, 57, and 59 (June 1960 to November 1962).

than of adult tunas (Yabe et al., 1958), and because it was not possible to sample all the fishes landed at the markets, emphasis was placed on sampling the spearfishes.

Other stomachs sampled were from fishes caught by longlining on four cruises of the "Charles H. Gilbert" during the period covered by this study and from fishes caught during the 1962 Hawaiian International Billfish Tournament held at Kona, Hawaii, from July 31 through August 4, 1962. The cruise tracks of the "Charles H. Gilbert" are shown in Figure 1.

#### IDENTIFICATION OF JUVENILE ALBACORE

As would be expected of specimens found in stomachs, our juvenile albacore specimens

were in various stages of digestion. Specimens that retained most of their flesh were easily recognized as scombrids by the body contours and shape of the head (Fig. 2). Aside from the general shape, few of the external features of the specimens had escaped digestion sufficiently to be of any use in species identification. However, this was not a serious handicap, since the hard parts of the fish were relied upon for identification. In two of the specimens practically all of the flesh had been digested away and all that remained were the bony parts, but even these fish could be identified as albacore.

Yabe et al. (1958) discovered a striking vertebral character that is distinctive for albacore and used it in identifying juvenile albacore as

small as 12.4 cm in standard length. This character is the laterally flattened shape of the haemal spine of the first caudal vertebra (first elongate haemal spine) which is unique to albacore. It is interesting to note that although several investigators have studied the anatomy and morphology of albacore in great detail, the significance of this character was not recognized by them. Recently, Matsumoto (1963) investigated this structure in detail and showed conclusively that among the tunas it is only found in albacore.

The 12 juvenile albacore reported on here were identified on the basis of this character (Fig. 3). The flat haemal spine was readily observable in all of the specimens, the smallest of which measured an estimated 61 mm in standard length. The width of the spine was from about 1.3 to 2.3 times the width of the haemal spine following it. Furthermore, the juveniles possessed other albacore characters. As

in adults, the juveniles had  $7-9 + 1 + 19-21 = 27-30$  gill rakers and 39 vertebrae (18 pre-caudals and 21 caudals).

#### DESCRIPTION OF JUVENILE ALBACORE

Although the specimens were partially damaged by digestion, counts and measurements were made on the juveniles whenever they could be made accurately (Table 1).

The shape of the juveniles is more or less fusiform. Each jaw has a single row of small teeth. Villiform teeth are present on the palatines and vomer. The snout is short and somewhat pointed; the mouth is moderate. The vertebrae number  $18 + 21 = 39$ , including the urostyle. The first closed haemal arch is on the 10th vertebra. In two specimens the bones producing the arch on the 10th vertebra are in contact but not fused; in three specimens the arch is damaged. The angle made by the first closed haemal arch and the vertebral axis is



FIG. 2. Juvenile albacore 184 mm in standard length found in the stomach of a blue marlin caught off Kona, Hawaii, August 1, 1962. (The last few vertebrae became detached from the rest of the fish subsequent to measurement and are not shown in the photograph.)



approximately  $75-90^\circ$ . The first ventrally projecting parapophysis is on the 7th–9th vertebrae.

The posterior margin of the basioccipital, when viewed laterally, makes an angle of approximately  $90^\circ$  or more with the axis of the vertebral column in specimens smaller than 19 cm, and an acute angle in specimens about 25 cm and larger in standard length.

The intestine has the two folds characteristic of Thunnidae (Godsil and Byers, 1944).

Only one specimen had its first dorsal fin membranes intact; the fin membranes are covered with black pigmentation.

#### DISCUSSION

Although no attempt was made to study all the differences in the morphology of adult and juvenile albacore, a few of the more obvious ones were noted in some detail. As indicated earlier, the flattened haemal spine on the first caudal vertebra becomes definitive early in the

life of albacore, since a juvenile 61 mm in standard length already possessed this character. A meristic character that also develops early is the gill raker count, for all of the juveniles already possessed the full adult complement. However, several morphological features of adult albacore were still in their early formative stages in the juveniles. These were the orientation of the parapophyses on the vertebrae preceding the ninth vertebra, the angle the first haemal arch makes with the axis of the vertebral column, the orientation of the bones constituting the first haemal arch, and the shape of the posterior margin of the basioccipital.

According to Godsil and Byers (1944) the parapophyses preceding the first haemal arch extend laterally in adults. In juveniles the tips of the parapophyses on the vertebrae as far anterior as the seventh may project ventrally. Presumably, with growth the anterior parapophyses tend to straighten out and extend later-

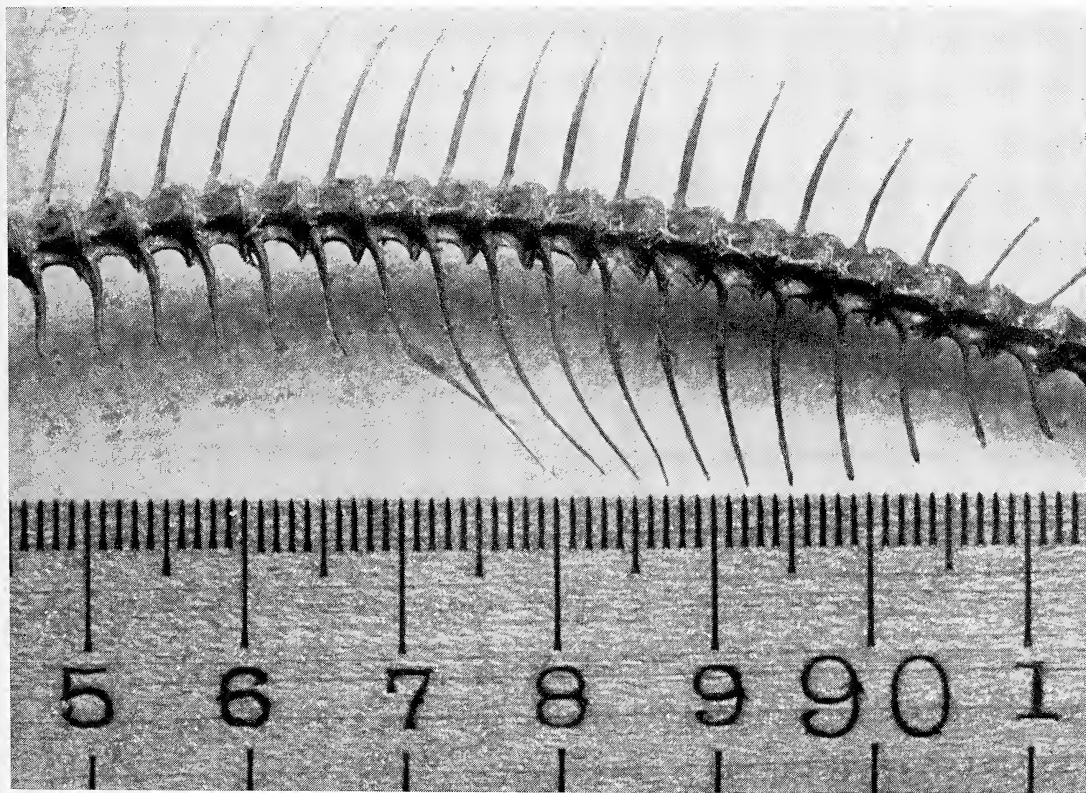


FIG. 3. Portion of axial skeleton of juvenile albacore showing unique, flattened haemal spine on first caudal vertebra.



TABLE 1  
COUNTS AND MEASUREMENTS MADE ON JUVENILE ALBACORE  
(Measurements in millimeters)

CHARACTER	SPECIMEN NUMBER						
	3	4	6	7	8	11	12
Standard length	—	—	88	74	184	—	—
Head length	—	—	—	19	48	—	—
Postorbital length of head	—	—	—	8	22	—	—
Iris diameter	—	—	—	6	—	—	—
Interorbital width	—	—	6	6	14	—	—
Snout length	—	—	6	5	—	—	—
Maxillary length	—	—	10	8	21	—	—
Snout to first dorsal origin	—	—	—	21	—	—	—
Snout to pelvic base	—	—	—	—	59	—	—
Longest pectoral ray	—	—	—	—	12	—	—
Gill rakers (number)							
Upper arch	7	7	7	9	8	8	7
Angle	1	1	1	1	1	1	1
Lower arch	20	20	19	19	21	20	20
Total	28	28	27	29	30	29	28
First dorsal fin	—	—	—	13	14	—	—

ally, starting with the anteriormost and ending with the parapophysis on the eighth vertebra. Actually, the tip of the parapophysis on the ninth vertebra projects ventrally and does not completely straighten out even in adults.

The first haemal arch in adult albacore makes an angle of 45° or less with the axis of the vertebral column, and the bones of the arch are flattened dorso-ventrally (Godsil and Byers, 1944). In juveniles the first haemal arch makes an angle of approximately 75–90°, with the greater angles generally occurring in the smaller specimens. The bones of the arch are flattened laterally. Evidently, as the albacore grows, the angle that the arch makes with the axis of the vertebral column becomes more acute. At the same time the posterior margins of the arch move forward and inward so that in adults the bones are compressed dorso-ventrally (Fig. 4).

Godsil and Byers (1944:84) state that the posterior margin of the parasphenoid and basioccipital, when viewed laterally, makes a prominent acute angle in adult albacore. However, a few paragraphs later (p. 85) they state that this margin may make an angle varying from slightly acute to somewhat obtuse. For our purpose, this character is perhaps best described as the angle the posterior margin of the basioccipital makes with the axis of the vertebral column.

When the cranium is viewed from the side, this angle is acute in adult albacore. In small juveniles this angle is obtuse, but with growth it changes to approximately 90° and finally to an acute angle (Fig. 5). A juvenile measuring 257 mm already possessed a skull similar to an adult. However, in a 184 mm specimen, the angle was still 90°. Therefore, it appears that this character becomes definitive in albacore at a standard length somewhere between 184 and 257 mm.

Yabe et al. (1958) found that juvenile tunas occurred more frequently in stomachs of spearfishes than of tunas. However, they also found that this varied according to area. Juvenile tunas occurred in stomachs of spearfishes and yellowfin tuna caught in low-latitude waters, but not in bigeye tuna. North of 30° N, however, juvenile tunas were also found in bigeye stomachs. Yabe and his colleagues suggested that this was due to a difference in vertical distribution of tunas and spearfishes, which in turn was related to the hydrography of the different areas. Although our sampling program was not designed to make such a comparison, most of our juvenile albacore were found in stomachs of spearfishes (Table 2). Six were found in the stomachs of five blue marlin, three in the stomachs of three striped marlin, two in the stomach of

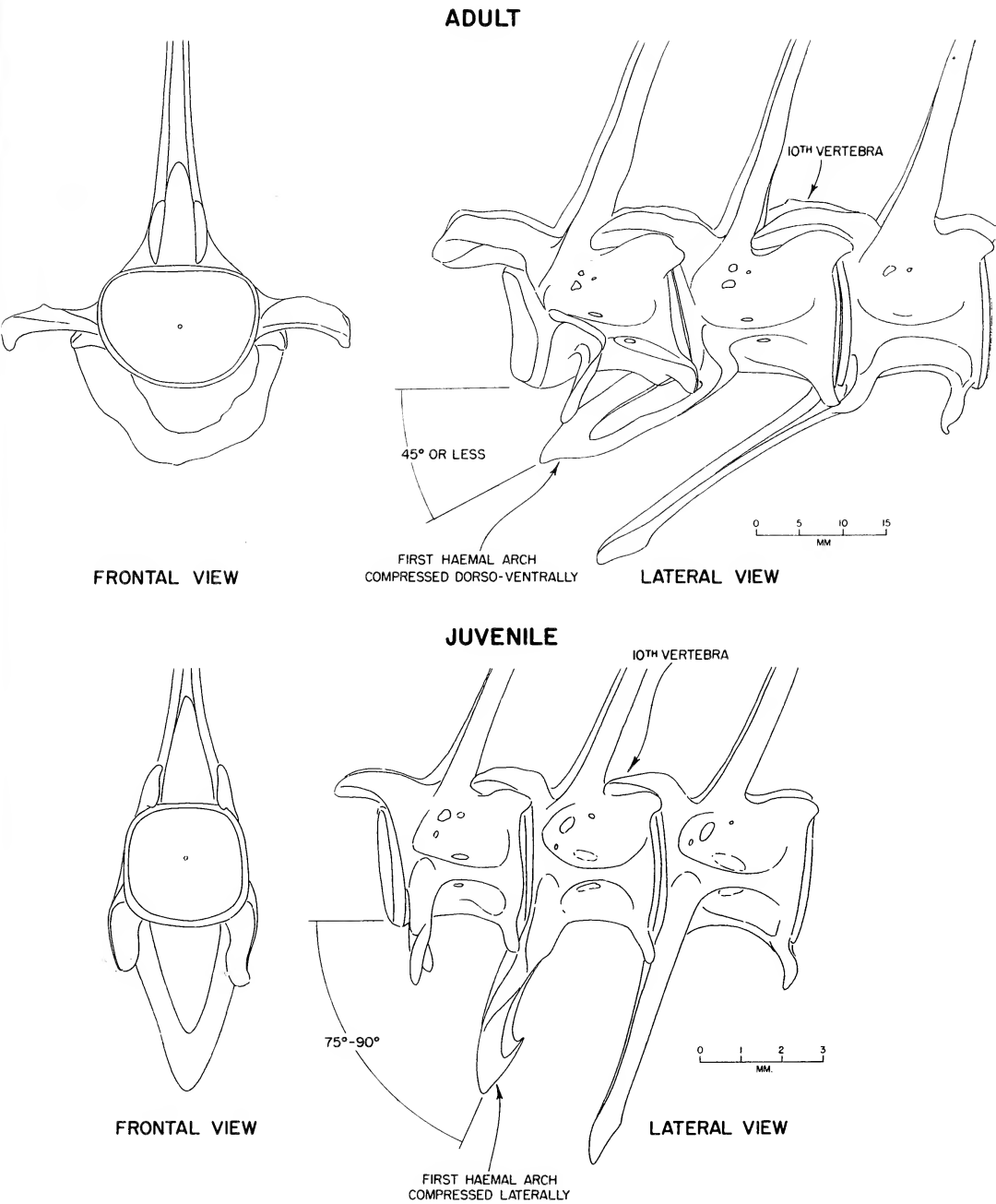


FIG. 4. First haemal arch of adult and juvenile albacore.

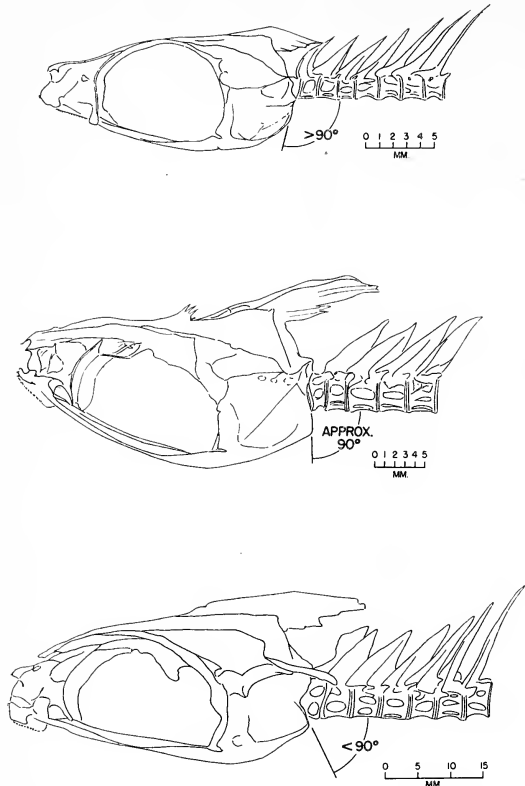


FIG. 5. Lateral view of skulls of juvenile albacore 88 mm (top), 184 mm (center), and 257 mm (bottom) in standard length.

a yellowfin, and one in the stomach of a wahoo (*Acanthocybium solandri*).

The occurrence of juvenile albacore in the Pacific Ocean is shown in Figure 6. Previously juvenile albacore were recorded from 18°38'N, 151°26' E and 20°57' N, 149°36' E in the western North Pacific and 18°44' S, 176°54' E, 18°58' S, 176°27' E and 20°50' S, 155°20' E in the central and western South Pacific (Yabe et al., 1958). The discovery of the 12 juvenile albacore reported here establishes a new eastward distribution record for juveniles in the Pacific Ocean. The known distribution of juvenile albacore now extends as far east as the Hawaiian Islands in the North Pacific and as far as 162° W longitude in the South Pacific.

Although the number of specimens is small, the discovery of juvenile albacore in these areas supports the findings of past studies on albacore spawning based on gonad condition and also provides positive evidence of spawning. It had been hypothesized that albacore in the North Pacific spawn in a broad area extending westward from the Hawaiian Islands (Ueyanagi, 1957; Otsu and Uchida, 1959). Similarly, in the South Pacific (also on the basis of gonad studies) Otsu and Hansen (1962) indicate that albacore may spawn in a broad area north of 20° S. It can be seen in Figure 6 that juvenile

TABLE 2  
JUVENILE ALBACORE FOUND IN STOMACHS OF PREDATORS

SPECIMEN NO.	DATE	LOCALITY	STANDARD LENGTH	PREDATOR
1	8-11-60	23°46' N, 171°02' E	131 mm*	blue marlin
2	8-11-60	23°46' N, 171°02' E	131 mm*	blue marlin
3	2-25-62	10°43' S, 178°46' E	85 mm	blue marlin
4	2-26-62	13°25' S, 179°15' W	61 mm*	yellowfin
5	2-26-62	13°25' S, 179°15' W	75 mm*	yellowfin
6	3-13-62	15°35' S, 171°16' W	88 mm	blue marlin
7	3-24-62	06°32' S, 162°45' W	74 mm	wahoo
8	8- 1-62	off Kona, Hawaii	184 mm	blue marlin
9	8-13-62	off Waianae, Oahu	135 mm*	striped marlin
10	9-13-62	off Waianae, Oahu	184 mm*	blue marlin
11	11- 2-62	off Waianae, Oahu	257 mm	striped marlin
12	11- 2-62	off Waianae, Oahu	283 mm*	striped marlin

\* Estimated.

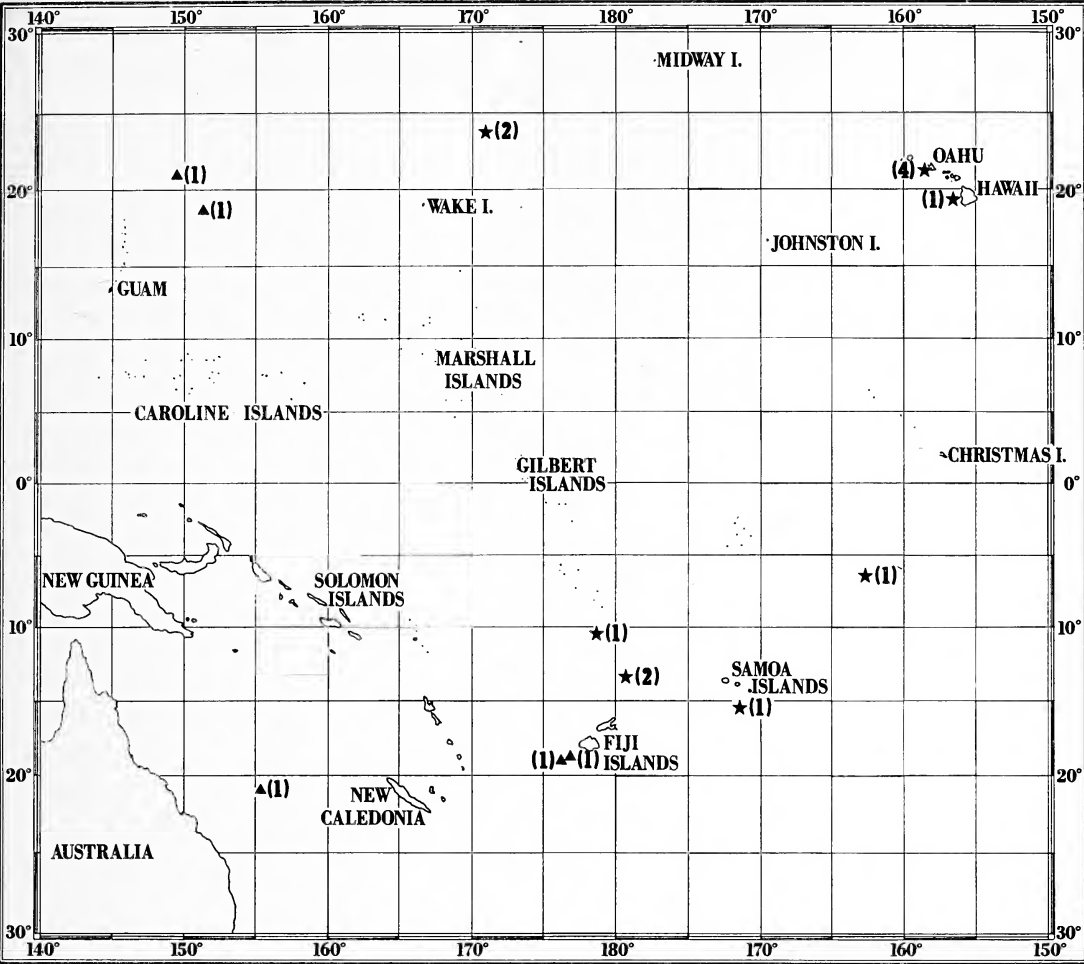


FIG. 6. Occurrence of juvenile albacore in the Pacific Ocean. Based on collections of Biological Laboratory, Honolulu, Hawaii (stars) and data in Yabe et al. (1958) (triangles). Figures in parentheses are numbers of specimens.

albacore have been captured in widely scattered areas in tropical and subtropical waters extending from approximately 150° E to 155° W in the North Pacific and 155° E to 162° W in the South Pacific. It would be interesting to discover whether albacore spawn randomly in these broad areas or whether there is concentrated spawning within them.

SUMMARY

Stomachs of large pelagic fishes collected during the period June 1960 through November 1962 were examined for the occurrence of juvenile albacore. The stomachs were obtained from

fishes landed by the Hawaiian commercial long-line fishery, captured during cruises of the research vessel "Charles H. Gilbert," and captured during the 1962 Hawaiian International Billfish Tournament at Kona, Hawaii.

Twelve juvenile albacore were discovered in the stomachs of predators: six from five blue marlin, three from three striped marlin, two from a yellowfin tuna, and one from a wahoo.

The juveniles were identified on the basis of the haemal spine on the first caudal vertebra, which in the albacore has a unique laterally flattened shape. The smallest specimen identified by this character measured an estimated 61

mm in standard length. Other supplementary characters confirmed the specimens as being albacore. The juveniles were described and counts and measurements were made.

The flattened haemal spine and full adult complement of gill rakers are developed relatively early in the life of the albacore. Certain other morphological features, including the angle the posterior margin of the basioccipital makes with the axis of the vertebral column, the orientation of the parapophyses on the vertebrae preceding the ninth vertebra, the orientation of the bones of the first haemal arch, and the angle the first haemal arch makes with the axis of the vertebral column, seem to develop more slowly and assume their adult form later in the life of the albacore.

A new distribution record for juvenile albacore was established with the discovery of these juveniles, demonstrating new or extending known spawning grounds for albacore in the Pacific Ocean. These captures of juvenile albacore support the conclusions of studies made on albacore spawning based on gonads, which indicated that albacore spawn in broad areas of the tropical and subtropical waters of the North and South Pacific Oceans.

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## Sexual Dimorphism in the Labrid Fish *Pseudolabrus celidotus* (Bloch and Schneider) 1801

J. H. CHOAT<sup>1</sup>

DURING A SYSTEMATIC STUDY of New Zealand fishes belonging to the genus *Pseudolabrus* Bleeker 1861, it was observed that one of the commonest species, *P. celidotus*, occurred in two distinct colour phases. This was first noted by Richardson (1848) who described the two colour variants as separate species. The subsequent literature did not recognise these as species, but merely as varieties, although the true relationship was not clarified. A study of populations of this species, both in the field and in the laboratory, revealed that the colour differences were due to sexual rather than environmental or geographic factors, and represented a moderately developed degree of sexual dimorphism. An attempt has been made here to examine the relative proportions of each colour phase in selected populations, the sequence of transition from one colour phase to the other, and the sizes at which transition occurs.

The specimens required for the study were obtained by a variety of quite orthodox methods, lining, spearing, trapping, and various netting techniques all being employed. Rotenone was successful in obtaining small specimens from enclosed rock pools but was less effective in open water.

The genus *Pseudolabrus* comprises a number of predominantly temperate water labrids, the majority of which occur in the coastal waters of New Zealand, Tasmania, and Southern Australia. They are almost completely absent from waters supporting coral reef formations although they have obvious affinities with the tropical Indo-Pacific labrids. *P. celidotus* shares the following characters with the majority of

other members of the genus: D. IX/11; A. III/10; operculum fully scaled; a series of small imbricate scales on the cheek; two pairs of anterior canines in each jaw; a posterior canine in each angle of the jaw; an inferior pharyngeal bone bearing a strongly developed anterior shaft; a continuous lateral line.

For the purposes of this study the colour phases were designated simply Phase A and Phase B. The characteristics of each follow. (In each case the descriptions have been furnished from fresh material.)

### *Phase A* (Fig. 1)

General body colouration ranging from pale whitish grey to yellowish green, usually with a black centre in each scale, these becoming more pronounced dorsally. Dorsum varies from dusky grey to black with the interorbital and occipital regions darker than the rest. Throat, isthmus, thoracic, and abdominal regions range from almost white to pale yellow, the sides of the abdomen often shaded by a reddish tint. A single prominent black blotch below the seventh to ninth dorsal spines, extending one scale row above and two scale rows below the lateral line, and covering the ninth to twelfth lateral line scales. Four dark transverse bars on the posterior portion of the body, often becoming indistinct in specimens exceeding 150 mm T.L. The first bar extends from just below the lateral blotch to a point level with the peduncle of the pectoral fin. The second extends from below the sixth to seventh dorsal rays to three or four scale rows below the midline of the body. The third extends from just below the termination of the dorsal fin to the region of the termination of the anal fin. The fourth bar is often diffuse and indistinct, and usually covers the last two or three transverse rows of scales on the caudal peduncle. Two prominent black postorbital bars, the first extending from

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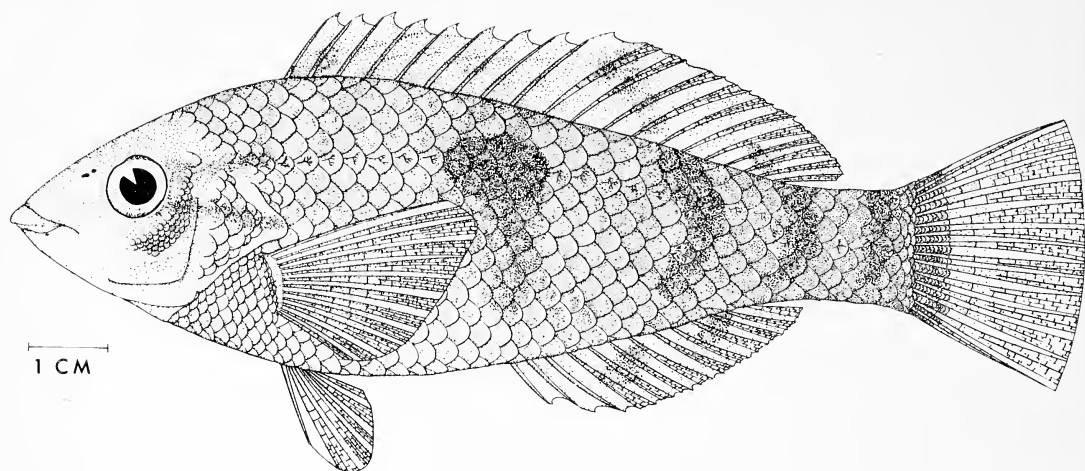


FIG. 1. *Pseudolabrus celidotus* (Female). Colour Phase A.

the mid level of the eye back to the level of the lateral line, the second extending from the lower posterior border of the eye across the operculum to the opercular membrane. A single black bar extending from the anterior margin of the eye to the edge of the maxillary.

Dorsal fin membrane pale to dusky, often becoming faintly yellowish where it invests the spines. Groups of small dark spots occur in the region of the first, second, fifth, and seventh spines, and in the first to fourth and eighth to ninth dorsal rays. Anal fin yellow to orange with two prominent black spots, the first on the

first to third rays and the second on the sixth to ninth rays. Caudal and pectoral fins range from very pale translucent yellow to colourless. Ventrals range from pale yellow to orange.

#### Phase B (Fig. 2)

Background colouration is generally similar to Phase A, although the dark tints on the dorsum and at the centre of each scale are not so pronounced. The body scales, especially in the anterior region, are often marked with bright blue ocelli which tend to fade rapidly

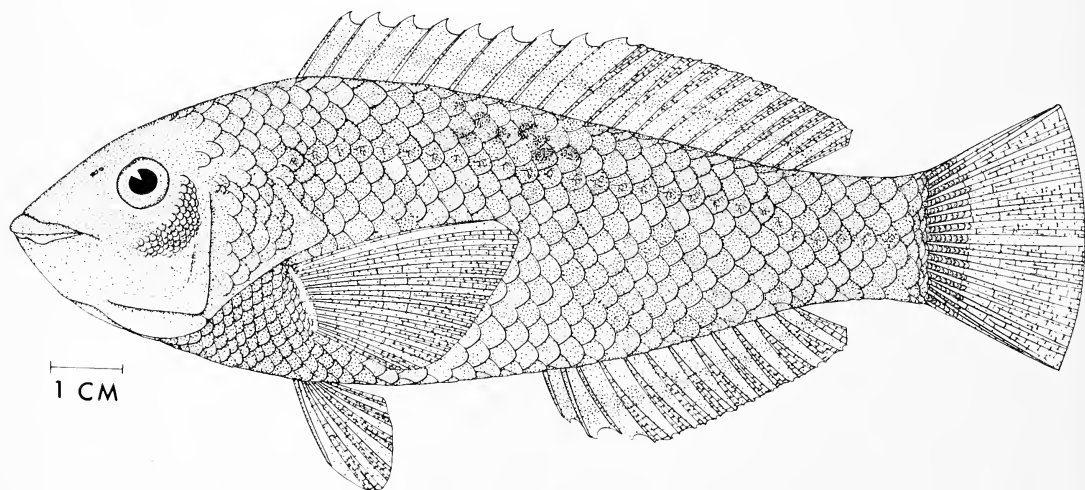


FIG. 2. *Pseudolabrus celidotus* (Male). Colour Phase B.

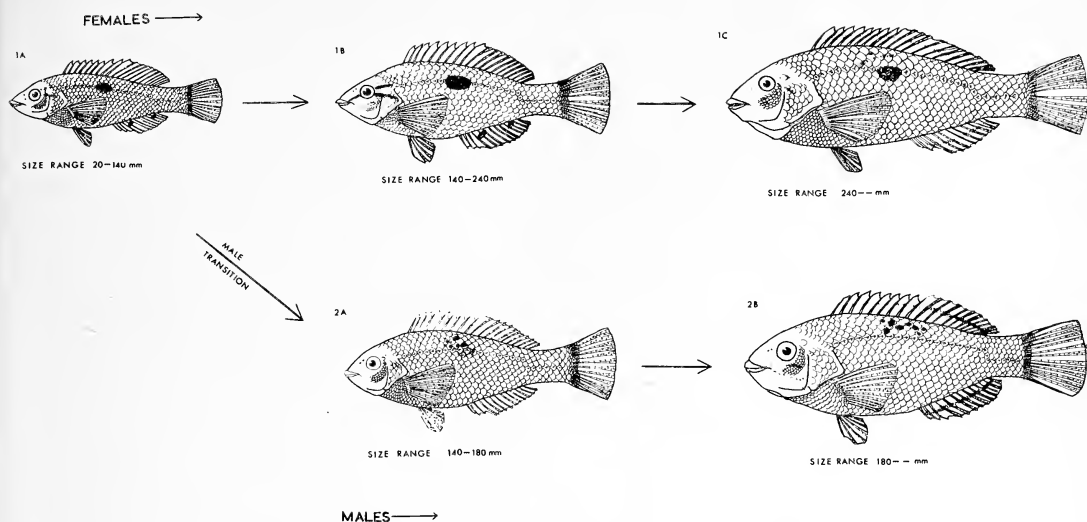


FIG. 3. General sequence of colour transition in males and females of *P. celidotus*. The lengths given must be regarded as being approximate only. It is inferred that sexual transition occurs in the upper limits of the 20–140 mm size range. 1C demonstrates the gradual development of the B colour pattern by females above 240 mm T.L. 2A shows the development of the B colour pattern at the expense of the A pattern in males between 140–180 mm T.L.

after death. The sides of the abdomen often with a pronounced reddish orange tint. Anterior and posterior orbital bars, black lateral blotch, anal fin spots, and the black transverse bars on body are lacking. A brilliant blue broken or unbroken line runs from the corner of the mouth to the lower anterior rim of the eye. This line may extend beneath the eye and across the upper series of cheek scales. A blue line extends horizontally from the lateral lobe of the lower lip to the vertical limb of the preoperculum. Both these lines may be reduced to a linear series of dots. Operculum with a scattering of bright blue dots. The dorsum with a series of black dots just above the lateral line, extending from the region just below the sixth dorsal spine to the second dorsal ray. These may tend to become slightly coalesced, and in larger specimens may extend some distance below the lateral line, giving the impression of an indistinct dusky transverse band.

The dorsal fin lacks the groups of dark spots seen in the A phase and is usually a pale yellowish green with a faint orange median longitudinal stripe. Anal fin lacking the two prominent dark spots but displaying a median longitudinal

yellowish stripe on a pale whitish green background. The ventrals are usually pale yellow.

#### *Transitional Stages Between the Two Colour Patterns (Fig. 3)*

On examination of a series of specimens ranging from 140 to 180 mm T.L., it was found that some exhibited colour patterns that were intermediate between the two phases. These comprised, in the main, specimens showing a definite B colour pattern but still retaining vestiges of the A pattern. The most common manifestation of this consisted of the dark lateral blotch being very faintly represented, with the cluster of black dots characteristic of the B phase strongly superimposed on it. In these specimens the suborbital and opercular blue linear markings were only faintly developed, and traces of the dark postorbital bars could still be detected. Transitional specimens invariably lacked the dark spots on the anal fin, displaying instead the longitudinal stripe of the B phase.

One specimen showing transitional characteristics was considerably larger (240 mm T.L.) than any others. This appeared to have a nor-



mal A colour pattern, although the anal spots were replaced by a longitudinal stripe. On closer examination faint traces of the black lateral dots and the blue opercular marks of the B phase could be detected.

Approximately 400 specimens were examined both in the field and in the laboratory. The results are presented below under the relevant headings.

#### *Correlation of Sex and Size With Colour Pattern*

Data concerning the size range, sex, and colour pattern of a range of specimens are presented in Figures 4 and 5. These data are based on an examination of the colour pattern and gonads of 399 specimens ranging from 71 to 255 mm T.L. This investigation revealed the following facts:

(1) Of the 399 specimens examined 280 were females, 105 males, and 14 could not be sexed due to decomposition of the viscera.

(2) The smallest female measured 71 mm T.L., the largest 240 mm T.L.

(3) The smallest male measured 104 mm T.L., the largest 255 mm T.L.

(4) Of the 280 females 279 exhibited a typical A colour pattern, and one specimen 240 mm T.L. exhibited a pattern transitional between A and B.

(5) Of the 105 males 94 exhibited a typical B colour pattern, six exhibited an A pattern, and four appeared to be transitional between A and B. (In Figure 4 it was found necessary to include specimens exhibiting transitional colour patterns as belonging to that group with which their pattern showed the strongest affinity.)

(6) Those exhibiting transitional colour patterns ranged from 141 to 177 mm T.L., except for one female 240 mm T.L.

(7) The six male specimens exhibiting an A colour pattern ranged from 104 to 149 mm T.L., and all contained well developed and apparently functional testes.

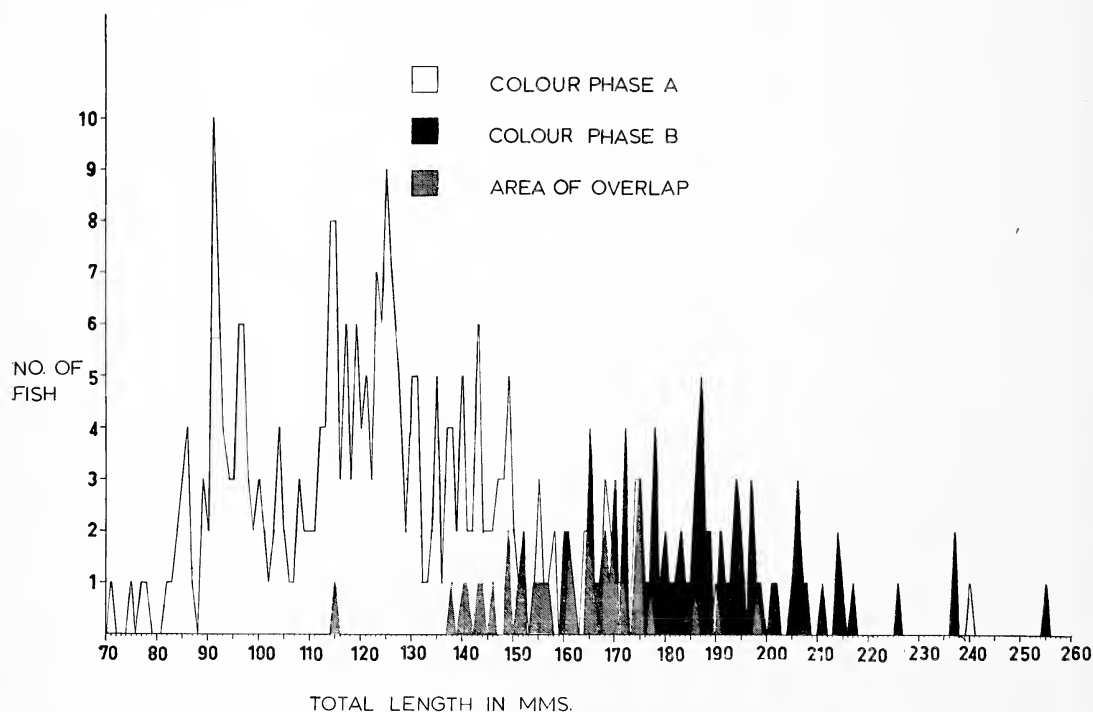


FIG. 4. Relationship of colour pattern exhibited to total length.

The main conclusions appear to be:

(a) A close relationship exists between the sex of each specimen and the colour pattern displayed.

(b) The B colour pattern is assumed by males on reaching a size of 140 to 180 mm T.L. A certain amount of variation can be expected as to the actual size at which the pattern becomes apparent. One male measuring 115 mm T.L. displayed a well developed B pattern.

(c) The males are capable of developing functional testes before the B pattern appears.

(d) Mature females in excess of 240 mm T.L. may assume the B colour pattern.

#### Paucity of Males

One of the most notable disclosures of this study was the paucity of males smaller than 104 mm T.L. Large numbers of specimens between 70 and 130 mm T.L. were examined, but of 201 individuals only four were males. Collections, using a variety of methods, were made over the full range of habitats known to be occupied by this species, and it is difficult to assume that the lack of small males

reflects a highly selective factor in the sampling techniques.

The most tenable explanation for the comparatively sudden appearance of males in the population is that this is a progyneous species, with all individuals commencing life as females. Such a possibility was indicated by Stoll (1955: 130), who studied the influence of hormones on the colour phases of the labrid *Thalassoma bifasciatum*. This situation may well obtain in *Gomphosus varius*, as Hiatt and Strasburg (1957:133) discovered no males smaller than 104 mm S.L.

Because this study was only an appendage to a systematic revision of the genus, there was insufficient time to initiate a conclusive study into the reproductive micro-anatomy and the effects of hormonal extracts.

In Figure 3 a general sequence of colour transition is presented. Inasmuch as no males smaller than 104 mm were discovered, and as those male specimens displaying an A colour pattern appeared to have functional testes, it was concluded that sexual transition generally occurs at approximately 130–140 mm, before the development of the B colour pattern.

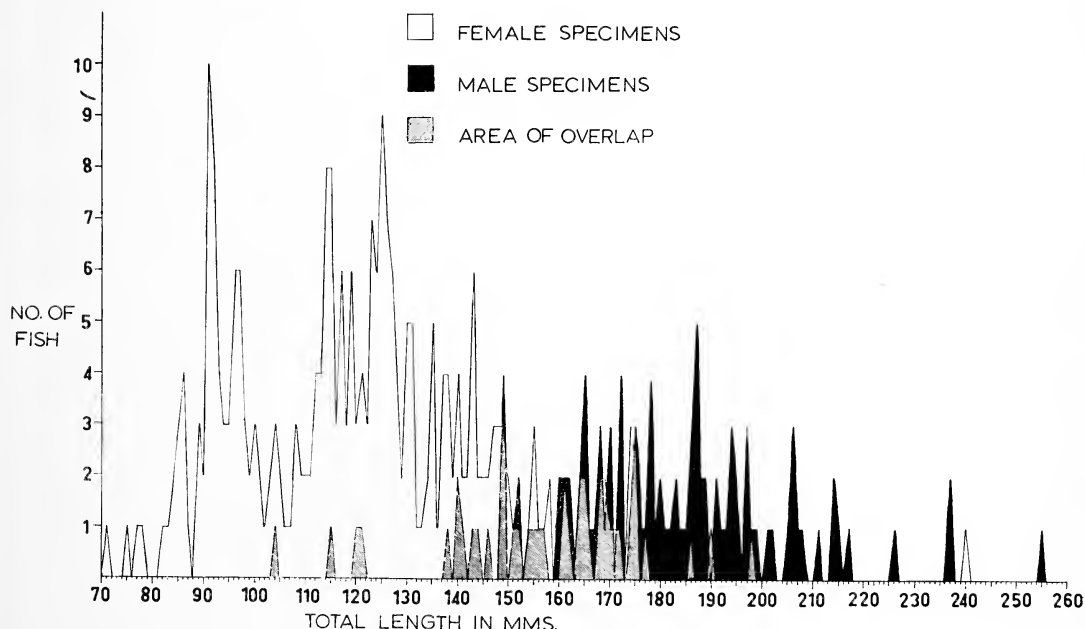


FIG. 5. Relationship of sex to total length.

### *Structural Changes Associated with Change of Colour Pattern*

These changes did not appear to be entirely due to sexual dimorphism and may have been influenced by developmental factors. The most striking changes are seen in the adult male, in which the profile of the head becomes increasingly obtuse. In many cases the convexity of the upper and lower profiles of the head is developed to such a degree that the appearance of the head is completely altered. Such changes also occur, although to a lesser degree, in large females. In large males the upper limb of the preoperculum is more nearly vertical than that of the female, this probably being due to the increased obtuseness of the snout and the proportional changes associated with it.

### *Disjunctive Distribution of the Sexes*

Adult males were usually obtained only from deeper water. The fact that shallow water collecting stations (especially over sandy bottoms in the vicinity of wharves and docks) revealed mainly females between 70 and 200 mm T.L. was thought at first to be due to a size selection factor imposed by the gear used. However, underwater observation confirmed the supposition that this habitat was populated mainly by individuals not exceeding 200 mm T.L. and displaying an A colour pattern. A few individuals approximately 200 to 240 mm T.L. displaying a B pattern were seen, but these were rather exceptional. Collection from deeper water (in the order of six fathoms), away from the vicinity of wharves and shoreline rocks, revealed the presence of a much larger population of large fish, the majority of them being males. This situation obtained in most habitats sampled but was more pronounced in sheltered bays and harbours with a uniform sandy bottom.

Hiatt and Strasburg (1957:133) record a rather similar situation in their work on *Gomphosus*. The adult male or "tricolor" phase was observed mainly in the deeper parts of the range and was uncommon even there. This was confirmed by the author while making field observations at Heron Island on the Barrier

Reef. Such a distribution is even more pronounced in the case of *Stethojulis strigiventer*, which Randall (1955) has shown to be sexually dimorphic. The immature and adult females bearing the "strigiventer" colour pattern were found to be common on the reef flat during both high and low water and, indeed, represented one of the most abundant species noted there. The adult male or "renardi" phase appeared to be almost absent from the reef flat and, although observed in reef crest pools and on the outer slope, was nowhere abundant.

### SUMMARY

(1) The temperate labrid fish *P. celidotus* occurs in two distinct colour phases which, for the purposes of this study, have been designated Phase A and Phase B.

(2) Specimens displaying a colour pattern transitional between A and B are observed.

(3) Examination of the colour pattern, gonads, and size range of a series of specimens indicates that the colour differences are due to sexual dimorphism.

(4) The B colour phase is characteristic of sexually mature males larger than 160 mm T.L.; the A colour phase is characteristic of immature and mature females smaller than approximately 240 mm T.L. and some mature males smaller than 160 mm T.L. Females larger than 240 mm T.L. may assume the B colour phase.

(5) A notable feature is the lack of males below 104 mm T.L. It is postulated that the species is progonous and that all specimens below 100 mm T.L. are females.

(6) The sexes have a disjunctive distribution, adult males being usually confined to the deeper parts of the range, usually in excess of 4-5 fathoms.

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# New Digenetic Trematodes from Hawaiian Fishes, I<sup>1</sup>

SATYU YAMAGUTI

THIS REPORT describes thirteen new species of digenetic trematodes, each of which represents a new genus. Although some of the digenetic trematodes of Hawaiian fishes have been worked out by American authors, such as Dr. H. W. Manter, Dr. W. E. Martin, and Mrs. M. H. Pritchard, my investigations on the same group of parasites, carried out under a grant (GB-78) from the National Science Foundation, have revealed that there still are large numbers of undescribed species. It is really surprising that American authors have failed to report the occurrence of didymozoid trematodes, which are not uncommon in the Hawaiian fishes. The major part of the results obtained in our survey of the Hawaiian trematodes will be published in two volumes of monographs, in which every species found by us will be treated taxonomically with related commentary.

Fishes were collected at the fish market of Honolulu by my assistant, Mr. Shunya Kamegai, and were examined by him for parasites as soon as possible.

The worms were fixed just overnight under appropriate cover glass pressure in acetic Schaudinn's solution; on the following morning, after removal from the slides in water, they were re-fixed in a sufficient quantity of acetic Schaudinn's solution, in which they were not allowed to stay for more than three hours (in order to facilitate removal of excess mercury by treating with iodine in 95% alcohol). Heidenhain's hematoxylin was consistently used for staining the specimens fixed in acetic sublimate, and 1% oxalic acid, when necessary, for bleaching the overstained specimens, the differentiation of which could not be adequately controlled by 2.5% solution of ferric ammonium sulfate. However, for the didymozoid trematodes which may be fixed with 10% formol solution, acetic

formol alcohol, or acetic Schaudinn's solution, with or without cover glass pressure; staining with Delafield's hematoxylin (commercial Delafield's with acetic acid added in 4%) is preferable in order to differentiate fully the male organs from the female organs; counterstaining with eosin is not necessary in this case. This method was also applied to massive trematodes of other families, which were, however, subjected to strong cover glass pressure by means of a wire compressorium.

The figures were drafted by Mr. S. Kamegai, with the aid of a camera lucida for the whole specimens but drawn freehand for particular structures. They were traced and finished for publication by Mrs. Ikuko Yamaguti.

The type specimens of all new species will be deposited in U. S. National Museum, Helminthological Collection at the Beltsville Parasitological Laboratory. In this report they are given accession numbers\* (headed by S. Y.) consecutive to those of the first report.

Thanks are due to the National Science Foundation, Dr. G. W. Chu, Department of Microbiology, University of Hawaii, Dr. W. A. Gosline, Department of Zoology, University of Hawaii, my assistant, Mr. S. Kamegai, and my wife, Mrs. Ikuko Yamaguti.

The new genera described herein are assigned to different families as follows:

## I. Lepocreadiidae Nicoll, 1935

### Bulbocirrinae n. subf.

#### 1. *Bulbocirrus aulostomi* n. gen., n. sp.

### Lepocreadiinae Odhner, 1905

#### 2. *Neoallopepidapedon hawaiiense* n. gen., n. sp.

## II. Acanthocolpidae Lühe, 1909

### Acanthocolpinae Lühe, 1906

#### 3. *Pseudacaenodera cristata* n. gen., n. sp.

## III. Hemiuridae Lühe, 1901

### Albulatrematinae n. subf.

#### 4. *Albulatrema ovale* n. gen., n. sp.

<sup>1</sup> Contribution No. 225, from Hawaii Marine Laboratory, University of Hawaii, Honolulu. Manuscript received March 16, 1964.

- Bunocotylinae Dollfus, 1950
5. *Pseudobunocotyla awa* n. gen., n. sp.
- Quadrifoliovariinae n. subf.
6. *Quadrifoliovarium pritchardi*  
n. gen., n. sp.
- IV. Lobatovitelliovariidae n. fam.
7. *Lobatovitelliovarium fusiforme*  
n. gen., n. sp.
- V. Didymozoidae Poche, 1907
- Didymozoinae (Ishii, 1935)
8. *Lobatocystis yaito* n. gen., n. sp.
- Nematobothriinae Ishii, 1935
9. *Allonematobothrium epinepheli*  
n. gen., n. sp.
10. *Allometanematobothrioides  
lepidocybii* n. gen., n. sp.
11. *Metanematobothrioides opakapaka*  
n. gen., n. sp.
12. *Nematobothrioides kalikali*  
n. gen., n. sp.
13. *Neonematobothrium kawakawa*  
n. gen., n. sp.
1. *Bulbocirrus aulostomi* n. gen., n. sp.

Fig. 1 A-C

HABITAT: Small intestine of *Aulostomus chinensis* (local name "nunu"); Hawaii.

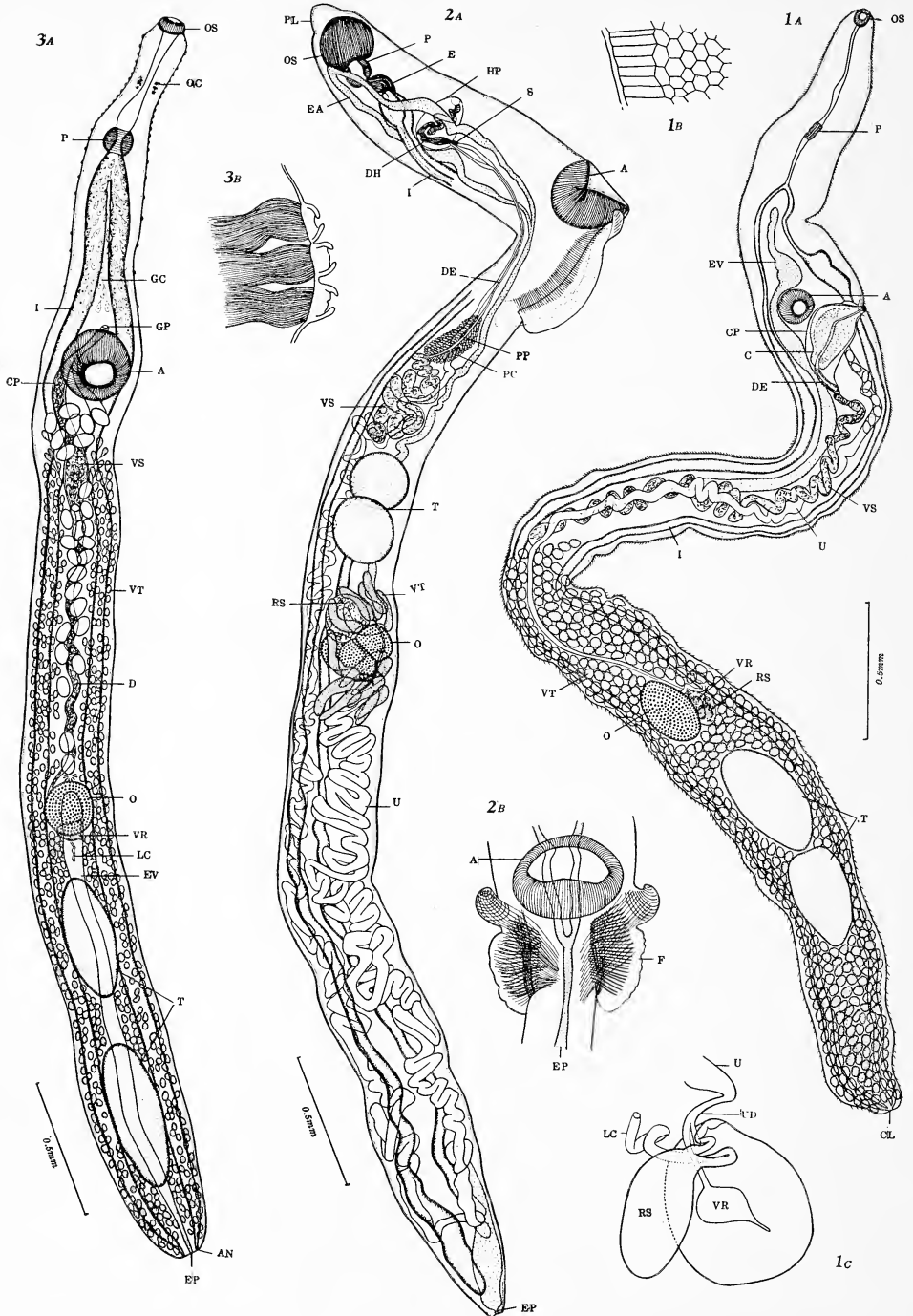
HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 19.

DESCRIPTION (based on eight whole mounts): Body long, slender, tapering anteriorly, 3.7-12.5 mm long, with maximum width of 0.2-0.55 mm in posterior third of body. Cuticle beset with minute spines, densely on greater anterior part of body, but sparsely on posterior third. Oral sucker ventroterminal, 30-80 × 40-90 μ; prepharynx slender, 0.2-0.7 mm long; pharynx cylindrical, narrow, muscular, 50-120 × 30-70 μ; esophagus slender, 0.1-0.3 mm long, bifurcating at a distance of 0.16-0.83 mm from acetabulum; left cecum greatly dilated at the beginning at level of acetabulum, and right cecum also dilated a little further behind in the type. At the posterior tip of the body is a shallow cloaca, into which the two ceca open separately, one on each side of the excretory vesicle. Acetabulum 0.08-0.15 × 0.08-0.17 mm, situated posterior to middle of anterior third of body.

Testes ellipsoidal, 0.3-0.8 × 0.19-0.43 mm, directly tandem in caudal third of body. Seminal vesicle tubular, very long, more or less swollen at proximal end, winding in median field between anterior end of vitellaria and cirrus pouch with its terminal portion differentiated into muscular ejaculatory duct enclosed in cirrus pouch. Cirrus massive, 0.1-0.45 × 0.05-0.2

ABBREVIATIONS USED IN FIGURES

A	acetabulum	M	metraterm
AN	anus	O	ovary
C	cirrus	OC	eye spot
CL	cloaca	OS	oral sucker
CP	cirrus pouch	P	pharynx
D	vas deferens	PC	prostatic cell
DE	ductus ejaculatorius	PL	preoral lobe
DH	ductus hermaphroditicus	PP	pars prostatica
E	esophagus	RS	receptaculum seminis
EA	excretory arm	SP	sphincter
EP	excretory pore	T	testis
EV	excretory vesicle	U	uterus
GC	gland cell	UD	uterine duct
GP	genital pore	VR	vitelline reservoir
HP	hermaphroditic pouch	VS	vesicula seminalis
I	intestine	VSE	vesicula seminalis externa
LC	Laurer's canal	VT	vitellarium



FIGS. 1-3. 1, *Bulbocirrus aulostomi* n. gen., n. sp. 1A, holotype, ventral view; 1B, part of wall of cirrus; 1C, ovarian complex, dorsal view. 2, *Quadrifoliovarium pritchardi* n. gen., n. sp. 2A, holotype, lateral view; 2B, postacetabular adhesive flaps, ventral view. 3, *Pseudacaenodera cristata* n. gen., n. sp. 3A, holotype, ventral view; 3B, cervical armature, lateral view.

mm, lined with closely packed, columnal structures and provided with a thin layer of circular muscle fibers, with a very narrow axial lumen which opens at the tip of the conical end of the cirrus. No prostatic complex. Cirrus pouch saccular,  $0.14\text{--}0.42 \times 0.08\text{--}0.3$  mm, with thin wall of mainly circular muscle fibers, almost completely occupied by cirrus and ejaculatory duct. Genital atrium not well developed, opening on left margin of body at level of posterior border of acetabulum.

Ovary oval,  $0.17\text{--}0.35 \times 0.12\text{--}0.26$  mm, situated in median line or a little out of it at junction of middle with posterior third of body, separated from anterior testis by vitellaria. Receptaculum seminis retort-shaped,  $0.14\text{--}0.2 \times 0.04\text{--}0.11$  mm, overlapping ovary on its dorso-lateral side. The germiduct arising from the anterior end or anterodorsal part of the ovary winds its way backwards or laterad and joins the seminal receptacle at its anterior end where the Laurer's canal is given off; then it unites with the vitelline duct to lead into the uterine duct. Laurer's canal winding, opening dorso-lateral to ovary. Uterus winding forward from in front of ovary alongside vas deferens; metratrem crossing cirrus pouch dorsally and opening into genital atrium immediately anterior to conical tip of cirrus; eggs elliptical, thick-shelled,  $46\text{--}65 \times 25\text{--}37 \mu$ . Vitelline follicles comparatively large, extending from posterior end of seminal vesicle to posterior extremity, confluent in median field between ovary and anterior testis as well as in posttesticular area; vitelline reservoir dorsal or lateral to ovary. Excretory vesicle tubular, middorsal, reaching as far forward as intestinal bifurcation; excretory pore terminal, forming cloaca.

**DISCUSSION:** This genus is characterized by the structure of the male terminal genitalia, the possession of a cloaca and an extremely long tubular seminal vesicle. Though resembling lepecreidiids in general anatomy, especially in the ovarian complex, extent of the vitellaria, and excretory vesicle, it differs from any of the known genera in the cirrus being developed as a massive organ and occupying almost the entire cirrus pouch and opening on the postacetabular margin of the body. The fact that the seminal vesicle develops outside the cirrus

pouch in the form of an extremely long winding tubule is also one of the important differential characters. I prefer to propose a new subfamily Bulbocirrinae, placing it near the subfamily Lepocreadiinae.

#### BULBOCIRRINAE n. subf.

**SUBFAMILY DIAGNOSIS:** Lepocreadiidae. Body slender, spinose. Oral sucker small, prepharynx long. Cloaca present. Acetabulum in anterior third of body. Testes tandem, in posterior part of body. Seminal vesicle tubular, very long, followed by muscular ejaculatory duct which is enclosed in cirrus pouch. Cirrus massive, enormous, occupying almost entire cirrus pouch. No internal seminal vesicle. Genital pore marginal, postacetabular. Ovary pretesticular. Uterus winding between ovary and cirrus pouch. Vitellaria posterior, not very extensive. Excretory vesicle tubular.

#### *Bulbocirrus* n. gen.

**GENERIC DIAGNOSIS:** Lepocreadiidae, Bulbocirrinae. Body tapering anteriorly, with maximum width in caudal third. Oral sucker small, ventroterminal; prepharynx very long; pharynx cylindrical; ceca opening into cloaca at posterior extremity. Acetabulum comparatively small. Testes directly tandem, posterior. Seminal vesicle very long, winding. No prostatic complex; ejaculatory duct muscular; cirrus massive, bulbous, occupying cirrus pouch together with ejaculatory duct. Genital atrium not well developed; common genital pore marginal, postacetabular. Ovary separated from anterior testis by vitellaria; receptaculum seminis and Laurer's canal present. Uterus long, winding; eggs thick-shelled. Vitellaria in posterior half of body. Excretory vesicle tubular, reaching to near intestinal bifurcation. Intestinal parasites of marine teleosts.

**TYPE SPECIES:** *B. aulostomi* n. sp., in *Aulostomus chinensis*; Hawaii.

#### 2. *Neoallopepidapedon hawaiiense*

n. gen., n. sp.

Fig. 7 A-B

**HABITAT:** Stomach and intestine of *Fistularia petimba*; Hawaii.



HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 20.

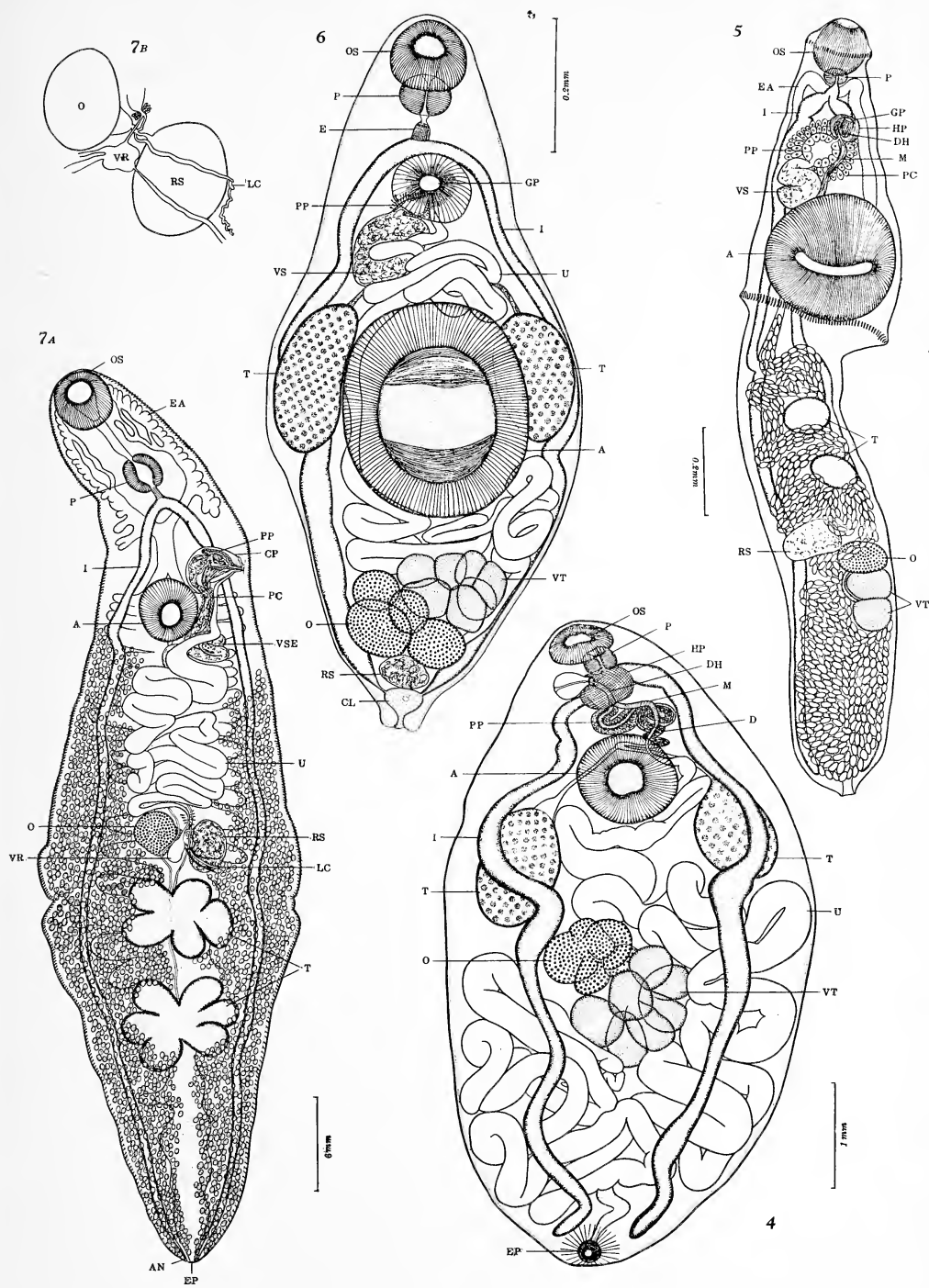
DESCRIPTION (based on 13 mature whole mounted specimens): Body elongate fusiform, with blunt extremities, 3.75–11 mm in length with maximum width of 0.8–2.3 mm in ovario-testicular region where the lateral margins are more or less irregularly crenulated; cuticle thick, beset throughout with minute spines. Oral sucker ventroterminal,  $0.23\text{--}0.5 \times 0.23\text{--}0.5$  mm; prepharynx  $0.13\text{--}0.55$  mm long; pharynx spherical,  $0.18\text{--}0.32$  mm in diameter; esophagus  $30\text{--}200$   $\mu$  long; ceca simple and wide anteriorly, but may be diverticulate on outer side in hind-body, opening outside separately, one on each side of excretory pore, at posterior extremity. Acetabulum  $0.28\text{--}0.64$  mm in diameter, situated at or near posterior end of anterior third of body.

Testes deeply lobed,  $0.18\text{--}1.3 \times 0.25\text{--}1.2$  mm, tandem; anterior testis usually 5-lobed, at posterior end of middle third of body, separated from ovary as well as from posterior testis by vitellaria; posterior testis usually 6-lobed, at anterior part of posterior third of body. Seminal vesicle tubular,  $50\text{--}170$   $\mu$  wide, closely winding posterodorsal to acetabulum in the fully gravid type, but extending farther backward in young individuals, a little to left of median line, with its anterior portion surrounded by prostate cells, whose ducts enter the cirrus pouch at its posterior end to discharge into the pars prostatica enclosed in the pouch; the anterior end of the seminal vesicle penetrates the posterior end of the cirrus pouch, and forms a definite, distally swollen, internal seminal vesicle which leads into the pars prostatica with a constriction or demarcation between. Pars prostatica muscular, bulbous, with its distal end differentiated into a short cirrus. Cirrus pouch saccular, thin-walled,  $0.2\text{--}0.6 \times 0.09\text{--}0.4$  mm, extending obliquely or transversely from anterosinistral edge of acetabulum to genital pore, containing distal end of external seminal vesicle, internal seminal vesicle, very strongly developed pars prostatica, numerous prostatic ducts coming from prostate cells surrounding distal portion of external seminal vesicle, and a short stout cirrus. Genital

atrium muscular, lined with thick cuticle, opening sinistrosubmarginally at pre-acetabular level.

Ovary subglobular to longitudinally elongated oval,  $0.06\text{--}0.56 \times 0.06\text{--}0.4$  mm, at or behind equatorial level, slightly to right of median line. Germiduct arising from left side of ovary, strongly constricted at its origin, giving off Laurer's canal just before joining seminal receptacle; seminal receptacle large,  $0.2\text{--}0.5 \times 0.15\text{--}0.4$  mm in fully mature specimens, situated to left of ovary, a little in front of anterior testis. Laurer's canal opening outside dorsal or immediately sinistral to seminal receptacle. Uterus tightly coiled in intercecal field between ovary and acetabulum; metraterm running alongside male terminalia. Eggs oval,  $44\text{--}54 \times 27\text{--}37$   $\mu$  in life. Vitelline follicles comparatively small, circumcecal, commencing at level of posterior end of acetabulum on the right, but a little more posteriorly on the left, intruding into space between ovary and anterior testis as well as into intertesticular space without meeting in median line, but almost confluent in posttesticular area; vitelline reservoir oval,  $85$   $\mu$  wide in the type, up to  $0.28 \times 0.18$  mm, situated ventrally between ovary and seminal receptacle. Excretory vesicle Y-shaped; its stem with numerous lateral diverticles reaching to intestinal limbs or overlapping them; in posttesticular area these lateral diverticles are simple, but the remaining are irregularly subdivided dendritically. Between the acetabulum and the ovary the diverticles anastomose with one another in median line in mature specimens, so that the primary median stem recognized in immature specimens is now replaced by anastomosing diverticles. Immediately behind the intestinal bifurcation the median stem divides into two lateral arms, each of which gives off an inner secondary branch communicating anteriorly with the main lateral branch of its own side; excretory pore terminal, not forming cloaca.

DISCUSSION: This new genus closely resembles *Allolepidapedon* Yamaguti, 1940, but the general body shape, the peculiar structure of the excretory vesicle, and the presence of two separate anal openings instead of the cloaca prevent its being identified with the latter genus. It is defined as follows:



FIGS. 4-7. 4, *Albulatrema ovale* n. gen., n. sp.; holotype, ventral view. 5, *Pseudobunocotyla awa* n. gen., n. sp.; holotype, ventral view. 6, *Lobatovitelliovarium fusiforme* n. gen., n. sp.; holotype, ventral view. 7, *Neoalolepidapedon hawaiiense* n. gen., n. sp. 7A, holotype, ventral view. 7B, ovarian complex, ventral view.

*Neallrolepidapedon* n. gen.

GENERIC DIAGNOSIS: Lepocreadiidae, Lepocreadiinae Odhner, 1905. Body elongate, fusiform, more or less crenulated laterally in hindbody, covered with spines. Oral sucker ventroterminal; prepharynx long, esophagus short, ceca opening outside, one on each side of excretory pore. Acetabulum comparatively small, at or near posterior end of anterior third of body. Testes lobate, median, tandem, in posterior half of body. Seminal vesicle tubular, winding, extending back of acetabulum to variable extent, with its distal portion surrounded by prostate cells, the ducts of which penetrate the posterior end of the cirrus pouch and empty into the pars prostatica. Cirrus pouch thin-walled, extending between acetabulum and genital pore, containing vesicula seminalis interna, well developed pars prostatica and stout cirrus. Genital pore marginal or submarginal, at a preacetabular level. Ovary pretesticular. Receptaculum seminis and Laurer's canal present. Uterus coiled between ovary and acetabulum. Metratrum differentiated. Eggs oval, numerous, moderately large. Vitelline follicles comparatively small, extending along ceca for their greater part. Excretory vesicle Y-shaped in fundamental pattern, but strongly diverticulate throughout its length, reticulate between ovary and acetabulum, with terminal pore, not forming cloaca. Gastro-intestinal parasites of marine teleosts.

TYPE SPECIES: *N. hawaiiense* n. sp., in *Fistularia petimba*; Hawaii.

3. *Pseudacaenodera cristata* n. gen., n. sp.

Fig. 3 A-B

HABITAT: Small intestine of *Conger marginatus*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 21.

DESCRIPTION (based on six whole mounts): Body slender, tapering anteriorly and narrowed in region of prepharynx,  $2.4-4.5 \times 0.3-0.42$  mm; a little swollen immediately behind oral sucker; the neck region from this swelling down to the acetabular zone is provided on each lateral margin and on the ventromedian field with irregular longitudinal rows of sharp-edged discoid cuticular projections, which are most prom-

inent in the postoral zone and gradually diminish posteriorly. Numerous strong parenchymatous muscles are attached to the base of each projection in this postoral area and fill the whole space between the body wall and the prepharynx, so that this portion probably functions as a powerful accessory attachment apparatus. Oral sucker terminal, bowl-shaped, with wide aperture,  $50-63 \times 78-110 \mu$ . Prepharynx  $0.23-0.35$  mm long, considerably enlarged just in front of pharynx, with a compact or dissociated eye spot on each side at about its middle. Pharynx barrel-shaped,  $60-100 \times 76-110 \mu$ , with wide lumen. Esophagus wide, about  $80-100 \mu$  long, bifurcating near middle of forebody. Ceca also wide in forebody; esophagus and anterior portion of ceca surrounded dorsally and ventrally by numerous gland cells which are irregular in shape and contain cytoplasmic granules, probably representing residue of the accessory digestive metacercarial glands. Both ceca opening independently at posterior extremity, one on each side of excretory pore. Acetabulum  $0.18-0.24 \times 0.17-0.25$  mm, situated at posterior part of anterior third of body.

Testes elliptical, tandem, in posterior third of body, separated one from the other by vitellaria; anterior testis  $0.22-0.42 \times 0.16-0.23$  mm, posterior testis  $0.28-0.51 \times 0.14-0.22$  mm. Cirrus pouch elongated claviform,  $0.34-0.5 \times 0.04-0.1$  mm, almost entirely occupied by seminal vesicle, not containing prostatic cells, in contrast with that of *Acaenodera placophora* Manter and Pritchard, 1960. No vesicula seminalis externa. The attenuated anterior portion of the seminal vesicle appears to join the metratrum dorsal to the acetabulum. Genital sinus tubular, opening midventrally on anterior border of acetabulum.

Ovary round,  $0.09-0.16$  mm in diameter, situated medianly a little anterior to fore testis, from which it is separated by the vitellaria. Laurer's canal opening almost middorsally between ovary and anterior testis. No seminal receptacle. Uterus winding in median field between ovary and acetabulum; eggs oval, moderately large,  $75-80 \times 52-58 \mu$  in life. Vitellaria extending uniformly in lateral fields around intestine from level of seminal vesicle to posterior extremity; vitelline reservoir com-

pact, overlapping posterior end of ovary. Excretory vesicle tubular, long, reaching to ovary, with terminal pore between two ani.

**DISCUSSION:** This genus is undoubtedly closely related to *Acaenodera* Manter and Pritchard, 1960, but differs from it distinctly in possessing discoid, cuticular, cervical projections instead of spines. I prefer to regard this difference as of generic importance. It is defined as follows:

*Pseudacaenodera* n. gen.

**GENERIC DIAGNOSIS:** Acanthocolpidae, Acanthocolpinae. Body slender, armed in cervical region with longitudinal rows of flattened conical or discoid cuticular projections both ventrally and laterally. Oral sucker terminal, bowl-shaped, prepharynx very long, widened posteriorly; pharynx barrel-shaped, esophagus very short, ceca opening outside by separate ani at posterior extremity. Acetabulum larger than oral sucker, less than one-third of body length from anterior extremity. Testes tandem, in posterior third of body. Cirrus pouch claviform, almost completely occupied by seminal vesicle, containing neither cirrus nor prostatic complex. Genital sinus tubular, opening medianly on anterior border of acetabulum. Ovary median, pretesticular. No seminal receptacle. Laurer's canal present. Vitellaria extending along ceca from level of seminal vesicle to posterior extremity; vitelline reservoir overlapping ovary. Uterus winding in intercecal field between ovary and acetabulum; eggs oval, medium-sized. Excretory vesicle long, tubular, with terminal pore. Parasitic in intestine of marine teleosts.

**TYPE SPECIES:** *P. cristata* n. sp., in *Conger marginatus*; Maui island, Hawaii.

4. *Albulatrema ovale* n. gen., n. sp.

Fig. 4

**HABITAT:** Swimbladder of *Albula vulpes* (local name "oio"); Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 22.

**DESCRIPTION** (based on 20 strongly flattened, whole mounts): Body subglobular to oval or pyriform, 3.4–6.2 mm long, 2.5–4.5 mm wide in midregion. Cuticle smooth; outer circular and inner longitudinal subcuticular muscles well

developed; parenchyma loose-meshed, traversed by strong muscle bundles running in different directions. Oral sucker terminal,  $0.3\text{--}0.4 \times 0.5\text{--}0.7$  mm, directly followed by muscular pharynx  $0.3\text{--}0.35$  mm long by  $0.15\text{--}0.45$  mm wide. Esophagus very short; ceca wide, undulating, ventrolateral or ventral to testis, lateral or ventral to ovary and vitelline gland, and ventral to uterus, terminating at posterior extremity, one on each side of excretory vesicle. Acetabulum  $0.6\text{--}0.85 \times 0.65\text{--}0.98$  mm, situated at posterior half of anterior third of body.

Testes oval,  $1.0\text{--}1.5 \times 0.54\text{--}1.1$  mm, placed almost symmetrically posterolateral to acetabulum; vas efferens arising from anterior end of each testis, joining together in median line dorsal to anterior part of acetabulum; vas deferens narrow proximally, but becoming wider and strongly muscular, forming a conspicuously winding or convoluted mass which is sharply delimited from the surrounding parenchyma by a capsule of apparently muscular element anterodorsal to acetabulum; seminal vesicle absent; pars prostatica sigmoid, strongly muscular, surrounded by well-developed prostate cells which are sharply delimited from the surrounding parenchyma by a distinct capsule of connective (?) or muscular fibers, joining metratrem at its anterior end to form eversible hermaphroditic duct. When everted, this duct forms a smooth bulbous prolapsus  $0.27\text{--}0.4$  mm wide and projecting out of the genital pore ventral to the pharynx. Hermaphroditic pouch bulbous,  $0.33\text{--}0.5 \times 0.45\text{--}0.5$  mm, consisting of a compact mass of longitudinal and circular muscles. Whether there is a genital atrium or not could not be ascertained.

Ovary  $0.45\text{--}1.15 \times 0.6\text{--}1.2$  mm, divided into four or five globular to oval lobes, situated close to center of body, a little to right or left of median line. Shell gland complex immediately posterolateral to ovary. Uterus coiling at first on right side of body posterior to right testis, dorsal to right cecum, then crossing over to left side across excretory vesicle ventrally, and winding on left side of body posterior to left testis, dorsal to left cecum, finally occupying space between ovary and acetabulum, and between acetabulum and left testis; metratrem sigmoid, running ventral to convoluted vas deferens and

pars prostatica. Eggs oval,  $17-23 \times 8-13 \mu$  in life. Vitellaria immediately posterior or posterosinistral to ovary, divided into six or seven, rarely eight, oval to pyriform, rosette-shaped lobes, measuring as a whole 0.75–1.5 mm by 0.9–1.9 mm. Excretory vesicle Y-shaped, opening ventroterminally or actually ventrally at a postvitellarian level, depending on the degree of pressure applied on the body of the parasite; excretory arms united anteriorly dorsal to oral sucker.

DISCUSSION: According to its general anatomy this new genus undoubtedly belongs to the family Hemiuridae, but cannot be referred to any known subfamilies under this family. I prefer to propose a new subfamily, Albulatrematinae, placing it near Lecithophyllinae Skrjabin and Guschansk., 1954 (= Hysterolecithinae Yamaguti, 1958).

#### ALBULATREMATINAE n. subf.

SUBFAMILY DIAGNOSIS: Hemiuridae. Body subglobose, or oval to pyriform, without tail. Oral sucker and pharynx well developed. Ceca not united posteriorly. Acetabulum in anterior third of body. Testes nearly symmetrical, posterolateral to acetabulum. Distal portion of vas deferens strongly muscular, convoluted and enclosed in apparently muscular capsule. No seminal vesicle. Pars prostatica strongly muscular, surrounded by prostate cells which are sharply delimited from surrounding parenchyma by muscular capsule, joining metraterm to form hermaphroditic duct, which is enclosed in a massive muscular pouch, and which may be everted out of the genital pore in form of a bulbous prolapsus. Genital pore ventral to pharynx or esophagus. Ovary lobed, submedian, in middle third of body. Vitellaria rosette-shaped, postovarian. Uterine coils occupying all available space of hindbody; eggs oval, small. Excretory vesicle Y-shaped, with ventroterminal or ventral opening; arms united anteriorly.

#### *Albulatrema* n. gen.

GENERIC DIAGNOSIS: Albulatrematinae, with characters of subfamily. Parasitic in swimbladder of marine or brackish water fishes.

TYPE SPECIES: *A. ovale* n. sp., in *Albula vulpes*; Hawaii.

#### 5. *Pseudobunocotyla awa* n. gen., n. sp.

Fig. 5

HABITAT: Stomach of *Chanos chanos* (local name "awa"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 23.

DESCRIPTION (based on 10 whole mounts): Body cylindrical, without tail, 0.8–1.7 mm long, 0.14–0.35 mm wide at postacetabular ridge, which encircles the body. On each side this annular ridge, well provided with longitudinal subcuticular muscle bundles, may be a more or less prominent, blunt-pointed cone directed posterolaterad. Around the oral sucker is a collar-like ridge which, however, may be straightened out when the oral sucker is protruded, or shifted forward as a ring when the oral sucker is retracted. Oral sucker bowl-shaped, terminal,  $70-140 \times 70-120 \mu$ , directly followed by a small pharynx  $23-50 \times 35-60 \mu$ ; esophagus short, ceca widened anteriorly, terminating blindly near posterior extremity. Acetabulum large, prominent,  $0.19-0.37 \times 0.19-0.35$  mm, situated at junction of anterior with middle third of body.

Testes subglobose to oval,  $30-100 \times 32-110 \mu$ , postacetabular, slightly obliquely tandem in middle third of body, may or may not be separated by uterine coils. Vesicula seminalis tubular, sigmoid,  $25-70 \mu$  wide, overlapping anterodextral margin of acetabulum, with its tapering anterior end opening into pars prostatica. Pars prostatica rounded,  $40-70 \mu$  in diameter, lined with large vesicular epithelia and surrounded by large prostate cells which are delimited sharply from the surrounding parenchyma. At the distal end of the pars prostatica originates the wide eversible hermaphroditic duct which is lined with transversely wrinkled cuticle and enclosed in a muscular hermaphroditic pouch  $79 \mu$  in diameter in the type. Genital pore wide, median, opening immediately behind intestinal bifurcation.

Ovary subglobose to oval,  $42-70 \times 50-100 \mu$ , situated ventrally at anterior end of middle third of body. Receptaculum seminis large,  $60-120 \mu$  in greater transverse diameter, anterodorsal to ovary. Laurer's canal? Vitellaria

consisting of two compact oval masses measuring 37–60  $\mu$  by 46–100  $\mu$  and lying directly tandem immediately behind ovary; vitelline ducts united near their origin into a common duct which runs forward to the ootype situated dorsal to the ovary. Uterine coils descending to posterior extremity and then ascending, occupying all available space of hindbody; metratrem running forward ventral to pars prostatica and joining hermaphroditic duct at anterior end of pars prostatica. Eggs elliptical, 30–38  $\times$  13–20  $\mu$ . Excretory pore terminal; excretory vesicle tubular; excretory arms united anteriorly dorsal to pharynx or esophagus.

DISCUSSION: The present genus differs from *Bunocotyle* Odhner, 1928, in several important points, shown in Table 1.

*Genolinea ampladena* Manter and Pritchard, 1960, probably may be transferred to *Pseudobunocotyla*, although in this species the post-acetabular ridge represented by a mere transverse, ventral, cuticular line is stated by the authors to be present in three specimens and absent in three other specimens. It agrees completely with the present genus in general anatomy, especially in the terminal genitalia.

*Pseudobunocotyla* n. gen.

GENERIC DIAGNOSIS: Hemiuridae, Bunocotylinae.<sup>3</sup> Body cylindrical, without tail, with collar-like ridge around oral sucker and another immediately behind acetabulum. Oral sucker large, terminal; pharynx small, esophagus short,

ceca terminating separately near posterior extremity. Acetabulum very large, prominent, anterior. Testes tandem, postacetabular; seminal vesicle sigmoid, more or less overlapping acetabulum; pars prostatica large, surrounded by large prostate cells which are well delimited from the surrounding parenchyma. Hermaphroditic duct well differentiated, enclosed in muscular hermaphroditic pouch. Genital pore immediately postbifurcal. Ovary well separated from posterior testis by uterine coils; receptaculum seminis present. Vitellaria consisting of two compact masses situated directly tandem immediately behind ovary. Uterine coils reaching posterior extremity when fully developed. Eggs small, elliptical. Excretory vesicle tubular; arms united dorsal to pharynx or esophagus. Stomach parasites of marine or brackish water teleosts.

TYPE SPECIES: *P. awa* n. sp., in *Chanos chanos*; Hawaii.

6. *Quadrifoliovarium pritchardi* n. gen., n. sp.

Fig. 2 A–B

HABITAT: Stomach and pyloric ceca of *Naso unicornis* (local name “kala”); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 24.

DESCRIPTION (based on 17 whole mounts): Body elongate, cylindrical, smooth, 3.0–9.0 mm long by 0.2–0.6 mm wide, tapered at each extreme end. Mouth opening ventrosubterminally. Oral sucker 0.11–0.28  $\times$  0.15–0.29 mm, surmounted by rounded conical preoral lobe 40–90  $\mu$  thick, directly followed by well-developed pharynx 0.06–0.15 mm long by 0.08–0.15 mm wide; esophagus 80–220  $\mu$  long, provided with well-developed longitudinal muscle fibers. Ceca

TABLE 1  
DIFFERENTIATING CHARACTERISTICS OF *Bunocotyle* AND *Pseudobunocotyla*

CHARACTER	<i>Bunocotyle</i>	<i>Pseudobunocotyla</i>
Ceca	united posteriorly	terminating separately
Prostatic complex	poorly developed or lacking	very strongly developed
Vitellaria	single	double, tandem
Receptaculum seminis	absent (?)	present

<sup>3</sup> Subfamily diagnosis given in *Systema Helminthum*, vol. 1 (p. 267–268) must be emended so as to include *Pseudobunocotyla*.

comparatively wide, terminating at different levels near posterior extremity. Acetabulum wider than long, 0.23–0.42 mm in transverse diameter, situated in posterior half of anterior third of body, with a pair of muscular, auricular, ventrolateral lobes immediately behind; each of these lobes is constricted near its anterior end, 0.27–0.73 mm long, widest at middle of elliptical posterior portion; each lobe consists almost exclusively of dorsoventral muscle fibers, but some fibers which are located close to the point where the lobe is attached to the body are continued into the body parenchyma, so that the postacetabular lateral area of the body shows a dense marginal layer of strong transverse muscles.

Testes rounded,  $0.1\text{--}0.26 \times 0.11\text{--}0.3$  mm, directly tandem in ventral part of midregion of body. Seminal vesicle saccular, up to 0.13 mm wide immediately in front of anterior testis, whence it tapers and passes into a much coiled tubular portion. Pars prostatica 0.12–0.35 mm long, surrounded by a dense coat of prostate cells which is well delimited from the surrounding parenchyma. Ejaculatory duct following pars prostatica long and narrow, uniting with uterus at base of hermaphroditic pouch. Hermaphroditic duct muscular, smooth, convoluted in hermaphroditic pouch, up to 0.4 mm long when fully everted; hermaphroditic pouch elliptical to pyriform,  $0.08\text{--}0.26 \times 0.06\text{--}0.2$  mm, with comparatively thin walls of mainly longitudinal muscle fibers, a little posterior to intestinal bifurcation; genital pore midventral, 0.44–0.83 mm from head end.

Ovary divided into four spherical to oval, subequal lobes, measuring 0.13–0.4 mm longitudinally as a whole, situated ventrally at posterior part of middle third of body. Seminal receptacle voluminous, inverted retort-shaped, 0.08–0.4 mm in transverse diameter, situated immediately anterodorsal to ovary with its distal end produced backward. Shell gland complex immediately posterodorsal to ovary. Vitellaria divided into two rosette-shaped groups which are united together by a longitudinal collecting duct passing between the two ventral ovarian lobes, each group consisting of six or seven digitiform lobes totaling 12 or 14; anterior group

overlapping ovary and seminal receptacle; posterior group ventral to shell gland, with forwardly directed lobes overlapping ovary. Uterus descending near ventral cuticle down to cecal ends where it turns dorsad and ascends dorsal to the descending portion, ovary, seminal receptacle and testes. Anterior to the testes it runs alongside the male duct and finally joins the latter at base of hermaphroditic pouch where it is provided with a small sphincter. Uterine eggs numerous, elliptical, operculate, embryonated,  $25\text{--}30 \times 12\text{--}16 \mu$  in life. Excretory vesicle cylindrical,  $80 \times 70 \mu$  in lateral view in the type, with terminal pore; divided anteriorly into two wide lateral arms running forward and reaching to oral sucker or pharynx where they unite dorsally. In the young specimen 3 mm long the two lateral excretory arms are in direct contact with each other in median line behind the acetabulum.

**DISCUSSION:** From the internal anatomy of the genitalia it seems certain that this genus is related to *Lecithasterinae* Odhner, 1905. On the other hand it bears a certain resemblance to *Accacoeliidae* Looss, 1912, in which, however, the excretory stems are located dorsally and ventrally in the hindbody but laterally in the forebody and not united anteriorly. The paired postacetabular flaps should be regarded as an accessory adhesive organ without great taxonomic importance. I prefer, therefore, to propose a new subfamily *Quadrifoliovariinae* and place it near *Lecithasterinae* Odhner, 1905 and *Trifoliovariinae* Yamaguti, 1958.

#### QUADRIFOLIOVARIINAE n. subf.

**SUBFAMILY DIAGNOSIS:** *Hemiuridae*. Body long, slender, smooth. Preoral lobe prominent. Oral sucker and pharynx well developed; ceca terminating near posterior extremity. Acetabulum anterior, with a pair of muscular accessory adhesive flaps immediately behind. Testes tandem, ventral, in midregion of body. Seminal vesicle winding, prostatic cells well developed, both between acetabulum and anterior testis. Ductus hermaphroditicus enclosed in hermaphroditic pouch. Genital pore postbifurcal. Ovary distinctly lobed, ventral, posttesticular; seminal receptacle present. Laurer's canal? Vitellaria



consisting of two groups of digitiform lobes. Uterus first descending ventrally to near posterior extremity, then ascending dorsally. Excretory vesicle terminal, bifurcating into wide lateral arms united anteriorly.

*Quadrifoliovarium* n. gen.

GENERIC DIAGNOSIS: Hemiuridae, Quadrifoliovariinae. Body slender, tapered at both extremities. Oral sucker subterminal, directly followed by muscular pharynx; esophagus short, muscular; ceca terminating blindly near posterior extremity. Acetabulum transversely elongate, in anterior third of body; postacetabular muscular flaps constricted near anterior end. Testes directly tandem, in equatorial zone. Vas deferens swollen proximally immediately in front of anterior testis, but tapered and convoluted as it proceeds anteriorly; pars prostatica surrounded by compact layer of prostate cells, immediately anterior to winding tubular seminal vesicle; ejaculatory duct narrow, straight, running alongside terminal portion of uterus. Ductus hermaphroditicus slender, unarmed, muscular, extremely long when fully everted; hermaphroditic pouch elliptical to oval, thin-walled. Genital pore midventral, shortly postbifurcal. Ovary four-lobed, in anterior part of posterior half of body. Receptaculum seminis voluminous, immediately anterodorsal to ovary. Vitellaria divided into two (an anterior and a posterior) groups of digitiform lobes, largely overlapping ovary. Uterus extending backward and then forward dorsal to ovary and testes; metraterm not differentiated; eggs elliptical, small, embryonated. Excretory vesicle divided near posterior extremity into two wide lateral arms running forward and uniting dorsal to oral sucker or pharynx. Gastro-intestinal parasites of marine teleosts.

TYPE SPECIES: *Q. pritchardi* n. sp., in *Naso unicornis*; Hawaii.

(A posteriorly mutilated specimen of this species, collected by Dr. H. L. Ching, stained with carmine and mounted in balsam was kindly submitted to me by Mrs. Mary Hanson Pritchard, together with her sketches and description; for these I am greatly indebted, because this slide showed the anterior union of

the excretory arms and the structure of the terminal genitalia more clearly than my own specimens stained with Heidenhain's hematoxylin. This is why I prefer to dedicate the species in question to our esteemed fellow taxonomist, Mrs. Pritchard.)

7. *Lobatovitelliovarium fusiforme*

n. gen., n. sp.

Fig. 6

HABITAT: Intestine of *Ablennes bians* (local name "aha'aha"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 25.

DESCRIPTION (based on six whole mounts): Body fusiform, small, with posterior extremity projecting in form of a truncate cone, 0.72–1.13 mm long, 0.35–0.47 mm wide at level of acetabulum. Cuticle thick, smooth. No eye spots. Oral sucker subventral, 70–110  $\times$  80–140  $\mu$ , surmounted by inconspicuous preoral lobe, directly followed by muscular pharynx 23–80  $\mu$  long by 39–90  $\mu$  wide. Esophagus about 50  $\mu$  long, forming a barrel-shaped thickening of circular and longitudinal muscles posteriorly; ceca simple, passing dorsal to testes, opening into cloaca close to posterior extremity. Acetabulum large, largely postequatorial, 0.3–0.4 mm in diameter, with transversely elongated oblong aperture, the anterior and posterior margins of which are provided with semicircular lamellar muscle fibers.

Testes oval to elliptical, 0.1–0.21  $\times$  0.07–0.15 mm, situated symmetrically one on each side of acetabulum. Seminal vesicle ovoid, 0.14–0.2  $\times$  0.1–0.11 mm, medial to right cecum anterior to right testis and acetabulum, with its anterior end tapering anteriorly and passing into pars prostatica dorsally. Pars prostatica short, running dorsoventrally behind intestinal bifurcation and surrounded by prostate cells which form very thick compact layer, sharply delimited from the surrounding parenchyma. Neither ejaculatory duct nor cirrus differentiated. Genital atrium sucker-like, with midventral opening immediately behind intestinal bifurcation.

Ovary divided into four rounded to oval lobes, measuring 60–150  $\times$  130–190  $\mu$  as a whole, situated between two cecal ends, with



oval to transversely elongated seminal receptacle immediately behind. Vitellaria divided into six or seven compact lobes, measuring  $90\text{--}110 \times 130\text{--}170 \mu$  as a whole, situated immediately anteroventral to ovary, partly overlapping it and a little to left of median line. Laurer's canal? Uterus forming transverse loops between vitellaria and acetabulum as well as in front of acetabulum, finally opening into genital atrium from behind; eggs oval, small,  $16\text{--}19 \times 10\text{--}12 \mu$ . Excretory vesicle tubular, enlarged to form cloaca before opening terminally, divided dorsal to vitellaria into lateral collecting vessels, each of which runs forward along the lateral margin of the body.

**DISCUSSION:** As indicated by the name this new genus is characterized by the ovary and vitellaria being divided into compact lobes and lying in the caudal third of the body. From an anatomical point of view it bears a more marked resemblance to *Aerobiotrema* Yamaguti, 1958 than to any of the other known genera, although it is different ecologically. I would like to propose a new family Lobatovitelliovariidae with the genus as type, placing it near the Aerobiotrematidae.

#### LOBATOVITELLIOVARIIDAE n. fam.

**FAMILY DIAGNOSIS:** Digenea with large ventral acetabulum. Body small, tapering toward each extremity. Oral sucker and pharynx well developed; ceca opening into cloaca. Testes symmetrical, lateral, in acetabular zone. Vesicula seminalis and prostatic complex strongly developed. Genital pore midventral, postbifurcal. Ovary and vitellaria lobate, in caudal third of body. Uterus forming transversely elongated loops, metraterm not differentiated, eggs small, operculate. Excretory vesicle Y-shaped in general pattern, cloaca well developed. Intestinal parasites of marine fishes.

**TYPE GENUS:** *Lobatovitelliovarium* n. gen.

#### *Lobatovitelliovarium* n. gen.

**GENERIC DIAGNOSIS:** Lobatovitelliovariidae. Oral sucker subterminal, directly followed by pharynx; esophagus short, with bulbous swelling posteriorly; ceca running dorsal to testes, opening into cloaca at posterior extremity.

Acetabulum much larger than oral sucker, largely postequatorial. Testes one on each side of acetabulum. Seminal vesicle voluminous, pre-acetabular; pars prostatica surrounded by dense mass of prostate cells sharply delimited from surrounding parenchyma. No hermaphroditic duct. Genital atrium with sucker-like midventral opening behind intestinal bifurcation. Ovary divided into four lobes, close to posterior extremity. Seminal receptacle immediately post-ovarian. Vitellaria consisting of several compact lobes, immediately anteroventral to ovary. Uterus winding just anterior and posterior to acetabulum; eggs numerous, small, oval. Excretory vesicle tubular, narrow, enlarged to form wide cloaca at posterior extremity, bifurcating behind acetabulum; collecting vessels not uniting anteriorly. Parasitic in intestine of marine teleosts.

**TYPE SPECIES:** *L. fusiforme* n. sp., in *Ablennes bians*; Hawaii.

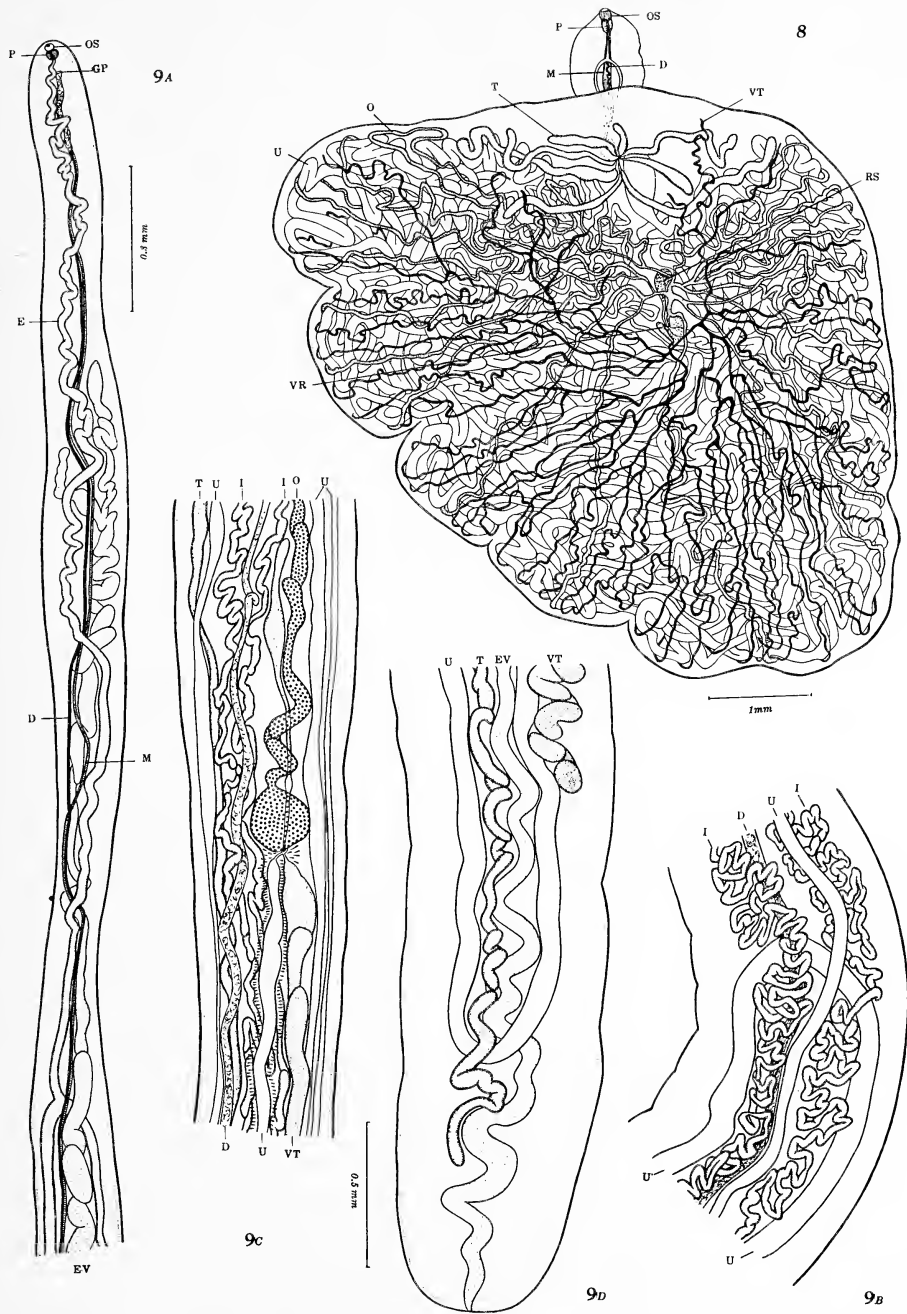
#### 8. *Lobatocystis yaito* n. gen., n. sp.

Fig. 8

**HABITAT:** Encysted in pairs in gill arch of *Euthynnus yaito* (local name "kawakawa"); Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S.Y. No. 26.

**DESCRIPTION** (based on five whole mounts): Body flat, approximately triangular, with its convex side usually divided into six hemispherical lobes, and its flat anterior edge in direct contact with the corresponding edge of its fellow-occupant of the cyst; the forebody arising from this side is pressed flat against the flat surface of the hindbody, another rather flat side of the hindbody being on the same plane as the corresponding side of the other partner, so that the two individuals are enclosed in an elongated, flattened hemispherical cyst. Forebody scoop-shaped, 1.5–2.6 mm in length, with maximum width of 0.74–1.05 mm at level of intestinal bifurcation. Oral sucker prominent,  $0.11\text{--}0.16 \times 0.12\text{--}0.18$  mm, directly contiguous to pharynx, latter  $0.14\text{--}0.2 \times 0.13\text{--}0.2$  mm; the two organs appear like a single organ. Esophagus slender, 0.2–0.5 mm long; ceca narrow in forebody, but inflated in hindbody and apparently terminating near posterior extremity.



FIGS. 8-9. 8, *Lobatocystis yaito* n. gen., n. sp.; holotype, dorsal view. 9, *Allometanematobothrioides lepidocybii* n. gen., n. sp. 9A, anterior part of paratype, dorsal view. 9B, region of anterior uterine loop of holotype, ventral view. 9C, region of genital junction of holotype, dorsal view. 9D, posterior extremity of holotype, dorsal view.

Testes divided into eight long, tubular, unbranched lobes which are arranged radially from posterior end of vas deferens at base of forebody, the length of the lobes varying from 0.5 to 1.3 mm, and the width from 0.09 to 0.15 mm in the type. Vas deferens winding forward along with metraterm and opening together with latter ventral to oral sucker.

Ovary tubular, slender, irregularly ramified in the central region, sending slender branches into each marginal lobe. It is not possible to make out how many branches there are, because of their being intertwined with uterine coils and vitelline tubules. In *Didymocystis* the ovarian tubules are confined to a particular portion of the hindbody, but in the present genus they extend throughout the hindbody without being confined to a particular region. Receptaculum seminis retort-shaped, 0.25 mm in diameter, situated near the point where the main ovarian tubes meet and join the vitellarian stem. Vitellaria divided into numerous branches, which finally reach the peripheral area of the hindbody, where they form loops ending blindly. Uterus strongly convoluted, looping back on itself many times close to surface of each marginal lobe as well as on other sides, but not forming a definite egg reservoir before leading into metraterm. Metraterm well provided with circular muscles, running straight forward in intercecal field of forebody. Eggs small, somewhat bean-shaped, thin-shelled,  $12.5\text{--}15 \times 7.5 \mu$ .

DISCUSSION: This new genus is characterized by the peculiar shape of the hindbody which is usually lobed on one side, the multiple testes being radially arranged in the anterior part of the hindbody, and the ovary, uterus, and vitellaria being intertwined throughout the hindbody. It is defined as follows.

*Lobatocystis* n. gen.

GENERIC DIAGNOSIS: Didymozoidae, Didymozoinae. Forebody scoop-shaped, hindbody flattened into triangular form, with one margin

usually lobed and the other two margins straight. Oral sucker contiguous with pharynx; esophagus slender, bifurcating at level of widest part of forebody. Ceca probably terminating near posterior end of hindbody. Testes divided into eight long, unbranched tubules radiating from junction of vasa efferentia in anterior part of hindbody. Vas deferens winding forward in forebody along with metraterm and opening together with latter ventral to oral sucker. Ovary divided into slender branches reaching to peripheral area of hindbody. Receptaculum seminis retort-shaped. Vitellaria tubular, very slender, branched, intertwined among ovary and uterus, though extending mostly in peripheral area. Uterus strongly convoluted, occupying all available space of hindbody, without forming egg reservoir before entering forebody; eggs very small, somewhat bean-shaped, thin-shelled. Encysted in pairs in gill arch of marine teleosts.

TYPE SPECIES: *L. yaito* n. sp., in *Euthynnus yaito*; Hawaii.

9. *Allonematobothrium epinepheli*

n. gen., n. sp.

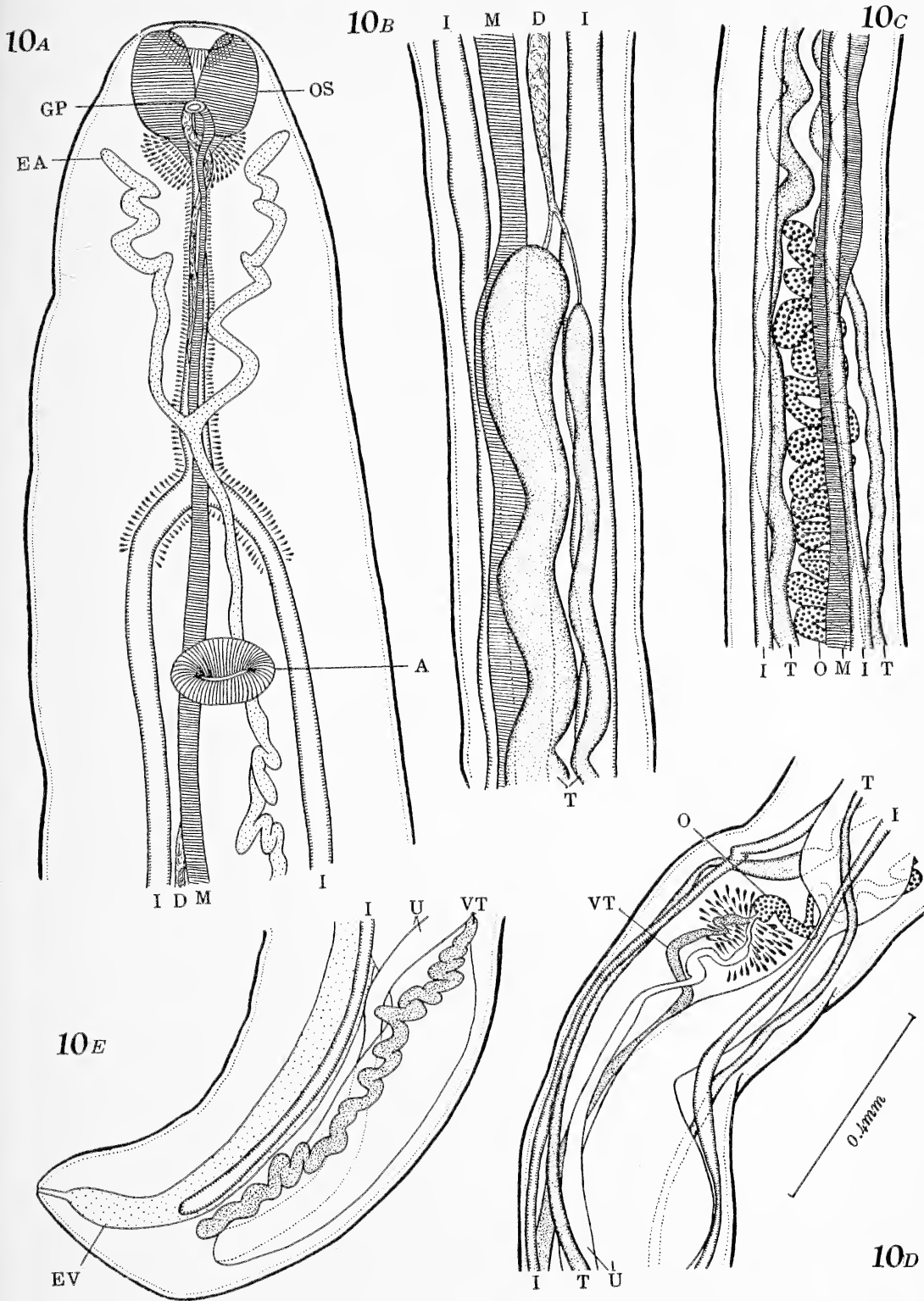
Fig. 10 A-E

HABITAT: Encysted in pairs in fins and underside of operculum of *Epinephelus quernus* (local name "hapu'upuu"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 27.

DESCRIPTION (based on seven whole mounts): Body slender, 70–365 mm long, up to 0.6–1.0 mm wide at irregular intervals where the ascending uterus is distended with eggs, somewhat swollen in acetabular region, blunt-pointed at posterior extremity. Oral sucker terminal, well developed,  $0.21\text{--}0.3 \times 0.24\text{--}0.3$  mm, directly followed by a funnel of transverse muscle fibers which in turn is surrounded by dense mass of glandular cells. Esophagus 0.5–1.0 mm long, provided with a layer of glandular cells appearing like accompanying cells, as is the very beginning of the intestinal limbs for a distance of about 0.2 mm in the type 183 mm

FIG. 10. *Allonematobothrium epinepheli* n. gen., n. sp. 10A, anterior extremity of holotype, ventral view. 10B, region of anterior part of testes of holotype, ventral view. 10C, region of anterior part of ovary of holotype, ventral view. 10D, region of genital junction of paratype. 10E, posterior extremity of holotype, lateral view.



long. Ceca simple, may reach posterior extremity, although more or less markedly atrophied posteriorly. Acetabulum prominent,  $0.11\text{--}0.18 \times 0.13\text{--}0.19$  mm, situated  $0.25\text{--}0.8$  mm behind intestinal bifurcation.

Testes two, juxtaposed, tubular, each commencing as a very narrow tubule  $6\text{--}30$  mm behind genital junction, more or less swollen at anterior end which lies at a distance of  $4\text{--}8$  mm from the head end, both usually terminating at slightly different levels. Vas deferens running alongside ascending distal portion of uterus. Genital pore median, ventral to oral sucker.

Ovary tubular, strongly winding in median field, unbranched, originating between two testes at a distance of  $4.5\text{--}20$  mm from head end,  $0.6\text{--}8.5$  mm behind anterior ends of testes. Germiduct short; no seminal receptacle. Genital junction  $14\text{--}60$  mm from head end,  $56\text{--}305$  mm from posterior extremity, dividing body in ratio of  $1:4\text{--}6$  ( $1:1.2$  in paratype  $132$  mm long). Uterine duct surrounded by shell gland cells, descending alongside vitelline gland, turning back on itself at posterior end of body or some distance (up to  $3.4$  mm) away from it, to be continued into final ascending uterus. The latter portion of uterus swollen at irregular intervals, differentiated into muscular metraterm some distance anterior to genital junction. Eggs bean-shaped,  $20\text{--}24 \times 8\text{--}10$   $\mu$  in life. Vitellarium tubular, winding irregularly, usually reaching to posterior extremity, originating  $3.0$  mm anterior to posterior extremity in one paratype in which the uterus also turns forward far away from the posterior extremity. In this specimen the posteriormost portion of the body looks like a slender tail. Excretory vesicle winding, bifurcating immediately in front of intestinal bifurcation; arms winding.

DISCUSSION: This genus is distinguished from the related genera according to the characters presented in Table 2.

### *Allonematobothrium* n. gen.

GENERIC DIAGNOSIS: Didymozoidae, Nematobothriinae. Body slender, very long, swollen at irregular intervals in gravid specimens. Oral sucker strongly muscular; pharynx practically

absent, though a funnel-shaped swelling is present at the anterior end of the esophagus. Esophagus and beginning of ceca surrounded by glandular cells. Ceca simple, may reach posterior extremity, more or less atrophied posteriorly. Acetabulum present. Testes paired, originating posterior to genital junction, terminating a short distance anterior to ovary. Ovary single, tubular, unbranched, intertesticular. No seminal receptacle. Uterus first descending, looping at posterior extremity alone. Vitellarium tubular, unbranched, extending between genital junction and posterior extremity. Excretory vesicle with terminal pore, bifurcating anteriorly into short arms. Encysted in pairs in fins or underside of operculum of marine teleosts.

TYPE SPECIES: *A. epinepheli* n. sp., in *Epinephelus quernus*; Hawaii.

### 10. *Allometanematobothrioides lepidocybii* n. gen., n. sp.

Fig. 9 A-D

HABITAT: Free in the periaortal connective tissue of *Lepidocybium flavobrunneum*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 28.

DESCRIPTION (based on two whole and one mutilated specimens): Body filiform, gradually tapered anteriorly to a blunt point,  $38$  mm in entire length, with maximum width of  $0.7$  mm in the somewhat flattened, intact, type specimen, one of the entire paratypes being  $30$  mm long. Oral sucker rounded, ventroterminal, rather cellular,  $23\text{--}25$   $\mu$  in diameter, followed directly by a muscular pharynx  $18\text{--}23$   $\mu$  long by  $23\text{--}30$   $\mu$  wide. Esophagus narrow, strongly winding,  $1.16$  mm long lineally in the type, but  $2.6$  mm long in the mutilated paratype. Ceca narrow, winding, rather convoluted and running in median field for greater posterior portion, but tending to atrophy posteriorly, terminating about  $12$  mm from posterior extremity in the type. No acetabulum.

Testes double, tubular, winding; in the type the anterior testis originates about  $5$  mm behind the genital junction and terminates  $6.3$  mm from the anterior extremity, whereas the posterior testis arises close to the posterior ex-

TABLE 2  
COMPARISON OF *Allonematobothrium* WITH RELATED GENERA

CHARACTER	<i>Nemato-bothrium</i>	<i>Allonemato-bothrium</i>	<i>Nemato-bothrioides</i>	<i>Metanemato-bothrium</i>	<i>Metanemato-bothrioides</i>	<i>Neonemato-bothrium</i>	<i>Allometanemato-bothrioides</i>
Body	encysted in pairs	encysted in pairs	free	free	free	free	free
Pharynx	present	absent	present	rudimentary	present	rudimentary	present
Esophagus	simple	simple	simple	simple	simple	unusually long, diverticulate, glandular	very long, winding, not diverticulate, not glandular
Ceca	simple	simple	simple	simple	simple	very narrow, convoluted	very narrow, convoluted
Acetabulum	present	present	absent	rudimentary	present	absent	absent
Testes	juxtaposed	juxtaposed	juxtaposed	juxtaposed	obliquely tandem	obliquely tandem	obliquely tandem
Ovary	undivided	undivided	undivided	divided	undivided	undivided	undivided
Uterus	first ascending, forming 2 loops	first descending, forming 1 loop	first descending, forming 1 loop	first descending, forming 3 loops	first descending, forming 1 loop	first descending, forming 3 loops	first descending, forming 3 loops

tremity (0.53 mm in the type, 0.16 mm in one entire paratype, from this extremity) and passes imperceptibly into the wide vas efferens which runs forward alongside the distal ascending uterus and unites with its fellow from the anterior testis a short distance anterior to the distal end of this testis; the vas deferens follows its median course all the way through alongside the distal uterus and finally opens midventrally together with the latter close to the anterior extremity a little behind the pharynx.

Ovary single, tubular, winding, unbranched, originating about 8 mm from the head end and terminating 2.2 mm from the same point in the type, where it is swollen into a pyriform mass 0.2 mm in diameter; the short germiduct arising from the posterior end of this ovarian mass soon joins the short ascending vitelline duct and leads into the uterine duct; the latter duct is at first rather straight but becomes twisted as it proceeds backward and is provided with a dense coat of shell gland throughout its descending course; after crossing the median ascending uterus, 3.2 mm behind the ovary in

the type, it leads into the straight narrow lateral ascending uterus. This ascending uterus turns backward across the ceca, distal ascending uterus, vas deferens, and excretory vesicle to take a descending course on the other side at a distance of 3 mm from the head end in the type. The descending uterus turns forward across the posterior testis and excretory vesicle 0.83 mm in the type and 0.24 mm in one entire paratype, from the posterior end to be continued as a final median ascending uterus, so that at a postovarian level there are seen four portions of the uterus, namely, descending uterine duct, proximal ascending, intermediate descending, and distal ascending uteri. Eggs bean-shaped,  $21-26 \times 12-16 \mu$ . Seminal receptacle very much elongated, extending forward from genital junction. Vitelline gland single, tubular, winding; originating near posterior extremity, 1.75 mm in the type and 0.6 mm in one entire paratype, from this end; it is straightened out distally to form an elongate vitelline reservoir about 0.1 mm wide in the type. Excretory vesicle tubular, winding, with almost terminal

pore, bifurcating into two unequal arms anteriorly at varying levels in esophageal region. Nerve commissure with a short anterior and a long posterior nerve trunk on each side, about 0.2 mm from head end in the type.

DISCUSSION: This genus is characterized by the following important features: (1) esophagus unusually long and winding; (2) ceca strongly convoluted for greater posterior part and running in median field rather than in lateral fields, atrophied posteriorly and not reaching posterior extremity; (3) testes tubular, double, obliquely tandem; extending greater part of body; (4) genital pore definitely postpharyngeal; (5) ovary single, tubular, unbranched, occupying greater middle portion of body; (6) uterus proper divided into three portions (proximal ascending, intermediate descending, and distal ascending); (7) no acetabulum. It bears a certain resemblance to *Metanematobothrioides*, but differs from it notably in all points except (5). It is defined as follows.

*Allometanematobothrioides* n. gen.

GENERIC DIAGNOSIS: Didymozoidae, Nematobothriinae. Body slender, very long, markedly tapered anteriorly. Oral sucker rudimentary, pharynx well developed. Esophagus long, narrow. Ceca strongly convoluted for their greater posterior part, tending to atrophy posteriorly, not reaching posterior extremity. Acetabulum absent. Testes double, tubular, winding, obliquely tandem, occupying greater posterior part of body. Genital pore ventromedian, definitely postpharyngeal. Ovary single, tubular, unbranched, occupying greater middle portion of body. Seminal receptacle present. Uterus first descending for a short distance, then ascending, turning backward in anterior part of body, finally turning forward at posterior extremity; eggs bean-shaped, small. Vitellarium tubular, extending from near posterior extremity to genital junction. Excretory vesicle with terminal pore, bifurcating anteriorly into two short arms.

Parasitic, free in tissues of marine teleosts.

TYPE SPECIES: *A. lepidocybii* n. sp., in *Lepidocybium flavobrunneum*; Hawaii.

11. *Metanematobothrioides opakapaka*

n. gen., n. sp.

Fig. 11 A-C

HABITAT: Submental connective tissue, inner surface and its opposite surface of operculum of *Pristipomoides microlepis* (local name "opakapaka"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 29.

DESCRIPTION (based on six entire specimens and a number of fragments): Entire body length 32-44 mm in immature specimens, 247 mm in the longest mature specimen, not completely hermaphroditic in young individuals. Body slender, slightly flattened dorsoventrally; anterior extremity more or less acute. Oral sucker terminal, 62-103  $\times$  75-117  $\mu$ ; pharynx 28-38  $\times$  30-38  $\mu$ . Esophagus simple, 0.35-0.8 mm long, bifurcating about halfway between pharynx and acetabulum. Ceca surrounded by gland cells at beginning for a distance of 0.2-0.3 mm, terminating at posterior extremity. Acetabulum 60-100  $\mu$  long by 80-110  $\mu$  wide, 0.8-1.1 mm from head end.

Testes paired, tubular, originating at different levels, one at posterior extremity and the other far away (10-65 mm) from it, terminating at a distance of 2.0-4.2 mm from head end. Vas deferens running alongside uterus and joining metraterm at common opening ventral to oral sucker.

Ovary winding, tubular, 15-43 mm long lineally, originating 4.3-10.4 mm from head end; distal end of ovary swollen and containing numerous yolk cells in the type 127 mm long; germiduct may be inflated as it receives the duct from the vitelline reservoir and then leads into the uterine duct which is lined with a layer of epithelia and surrounded by shell gland cells. Genital junction very variable in position, dividing body in ratio of 1:1-6. No definite sem-

FIGS. 11-12. 11, *Metanematobothrioides opakapaka* n. gen., n. sp. 11A, anterior extremity of holotype, dorsal view. 11B, region of genital junction of holotype, ventral view. 11C, posterior extremity of paratype, lateral view. 12, *Nematobothrioides kalikali* n. gen., n. sp. 12A, anterior extremity of paratype, ventral view. 12B, region of genital junction of holotype, ventral view. 12C, posterior extremity of holotype, ventral view.



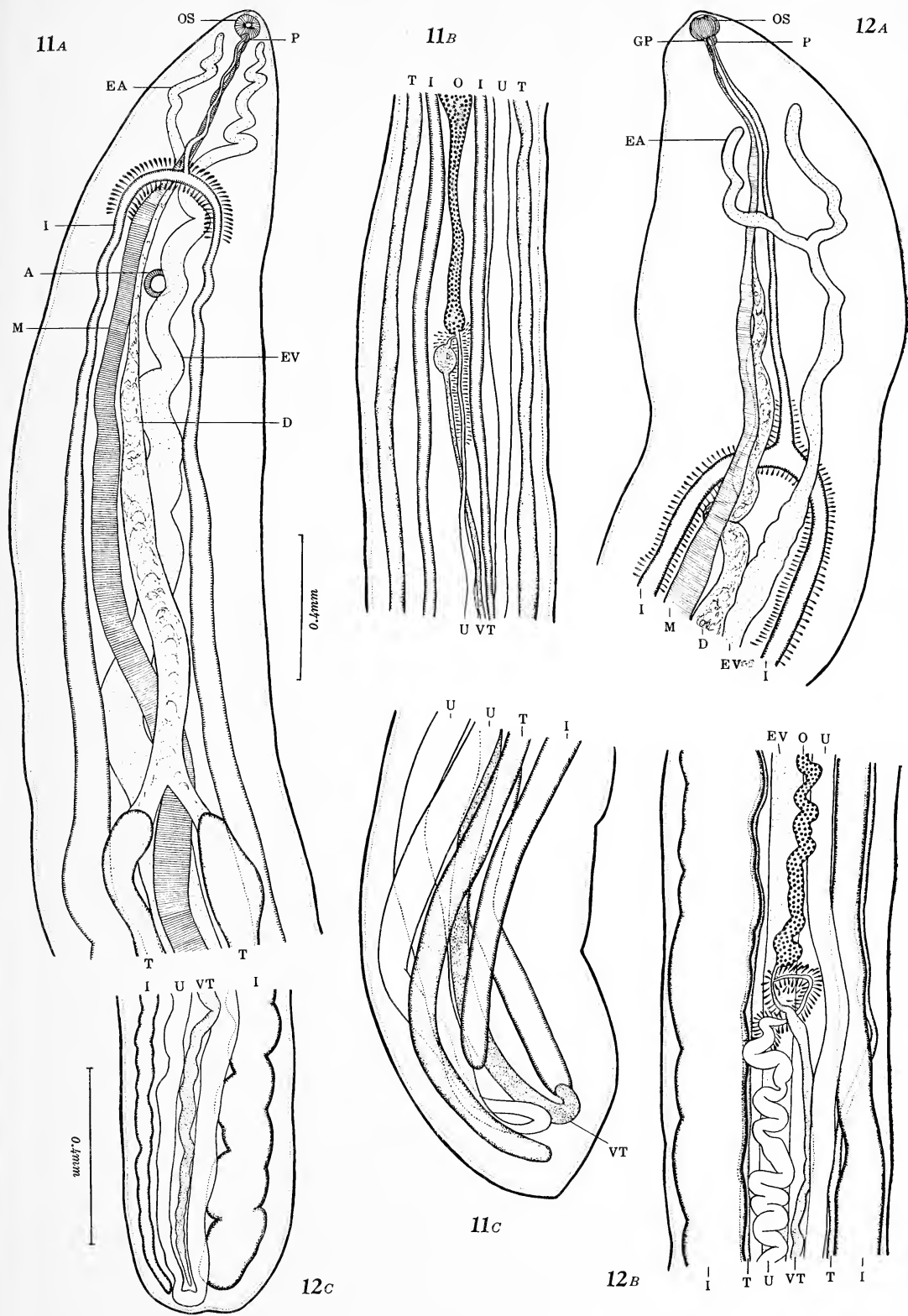




TABLE 3

DISTINGUISHING FEATURES OF *Metanematobothrium* AND *Metanematobothrioides*

CHARACTER	<i>Metanematobothrium</i>	<i>Metanematobothrioides</i>
Testes	turning back on themselves anteriorly	not turning back on themselves anteriorly
Ovary	divided	undivided
Receptaculum seminis	present	absent
Uterus	first descending, forming three loops	first descending, forming one loop

inal receptacle. Uterus proper first descending as far as posterior extremity, where it turns forward to be continued as ascending limb. Eggs bean-shaped,  $18-23 \times 11-14 \mu$ . Vitellarium a single, slender tube running straight backward from genital junction to posterior extremity along with uterus; just before joining the germiduct the vitellarium of the type is swollen into a bulbous reservoir  $50 \mu$  wide and distended with yolk cells. Excretory vesicle with terminal pore, bifurcating anteriorly into two short arms reaching to near nerve commissure.

DISCUSSION: This new genus presents several features by which it can be distinguished from the related genus *Metanematobothrium* (see Table 3).

#### *Metanematobothrioides* n. gen.

GENERIC DIAGNOSIS: Didymozoidae, Nematobothriinae. Body slender, very long. Oral sucker well developed, followed by small pharynx. Ceca surrounded by gland cells at beginning, terminating at posterior extremity. Acetabulum distinct, some distance behind intestinal bifurcation. Testes paired, tubular, sinuous, extending almost entire length of body in mature worms. Genital pore median, ventral to oral sucker. Ovary filiform, winding, unbranched, originating some distance behind distal ends of testes and descending to genital junction. No seminal receptacle. Uterus first descending, turning forward at posterior extremity; eggs elliptical, small. Vitellarium single, filiform, extending between ovary and posterior extremity. Excretory vesicle with terminal pore, bifurcat-

ing anteriorly into two short arms. Parasitic in marine teleosts.

TYPE SPECIES: *M. opakapaka* n. sp., in *Pristipomoides microlepis*; Hawaii.

#### 12. *Nematobothrioides kalikali* n. gen., n. sp.

Fig. 12 A-C

HABITAT: Free in subcutaneous connective tissue of opercular region of *Pristipomoides sieboldii* (local name "kalikali"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 30.

DESCRIPTION (based on four flattened entire specimens and a fragmented specimen): Body filiform, slender, 35-70 mm long, 0.4-0.5 mm wide, more or less blunt anteriorly but rounded at posterior extremity. Oral sucker subterminal,  $23-70 \times 74-86 \mu$ , pharynx  $35-58 \times 46-56 \mu$ ; esophagus simple, straight or sigmoid posteriorly, 60-100  $\mu$  long, ceca surrounded by glandular cells to a considerable extent at the beginning like the posterior portion of esophagus, terminating blindly at extreme posterior end of body. Acetabulum absent.

Testes very narrow, tubular, juxtaposed, originating one on each side a little behind genital junction, winding forward, turning inwards across ceca at about level of anterior end of ovary to come to lie medial to ceca, where they run forward parallel to each other, finally meeting in median line at a distance of 3.4 mm from head end in the type. From the point of union the vas deferens runs forward along with the uterus and unites with it into a short common duct which opens ventrally immediately behind the oral sucker.

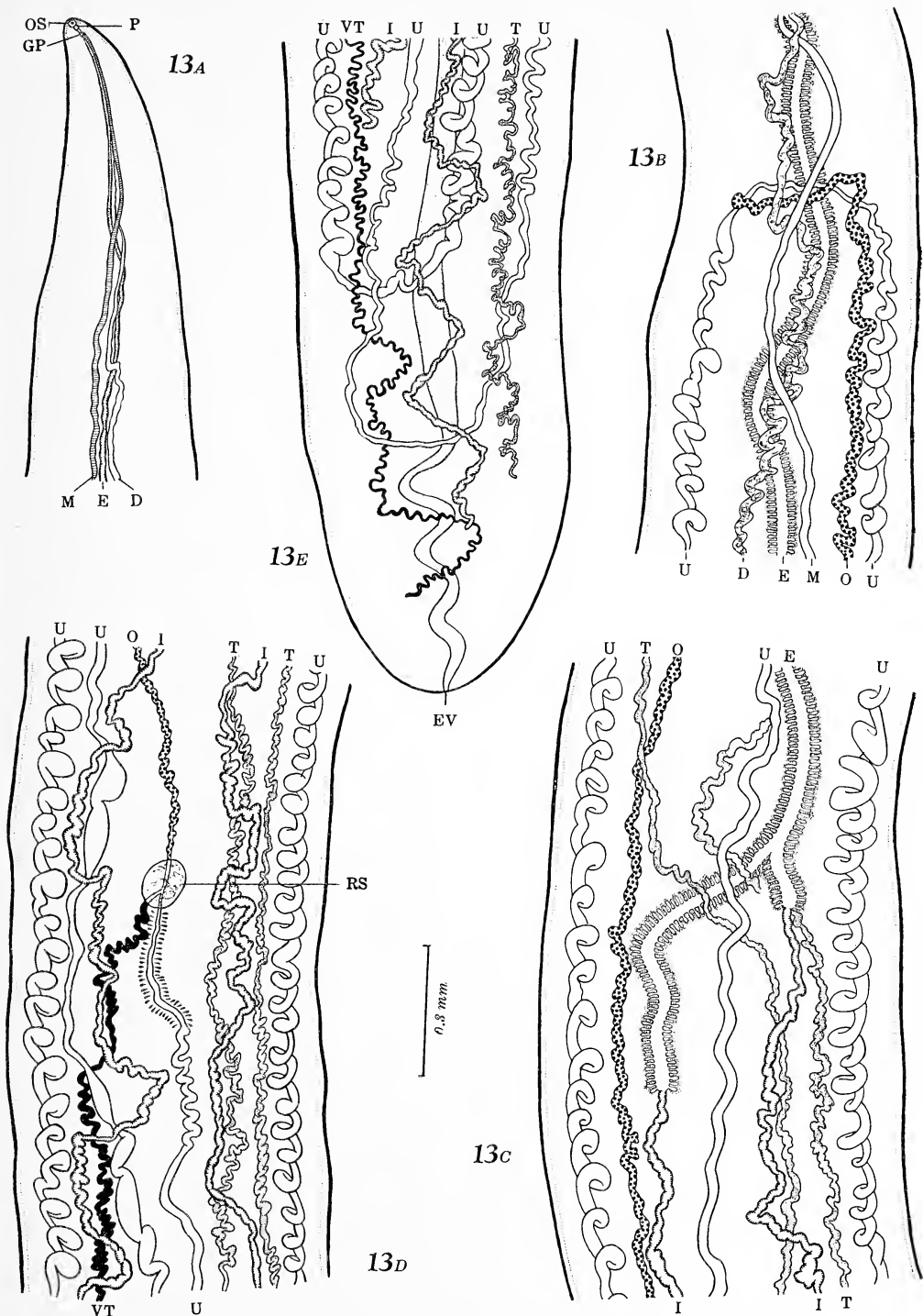


FIG. 13. *Neonematobothrium kawakawa* n. gen., n. sp. 13A, anterior extremity of holotype, ventral view. 13B, region of anterior part of ovary of holotype, ventral view. 13C, region of intestinal bifurcation of holotype, ventral view. 13D, region of genital junction of holotype, ventral view. 13E, posterior extremity of holotype, ventral view.

Ovary narrow, tubular, winding, arising at a distance of 4.2–10 mm from head end, but terminating at variable distances; in the type and one paratype the genital junction lies far anterior to the midbody, but far posterior to this point in the other two paratypes. Germiduct very short; seminal receptacle absent. Descending uterine duct strongly winding, surrounded by shell gland cells and studded with yolk cells for a distance of about 0.4 mm in the type, a short descending portion directly following it also strongly winding and distended with sperm. At the extreme posterior end of the body the descending uterus turns back on itself between the two cecal ends; the distal portion of the uterus runs straight forward along with the vas deferens; eggs oval,  $18\text{--}21 \times 11\text{--}14 \mu$ . Vitellarium narrow, tubular, extending from behind ovary to extreme posterior end of body.

DISCUSSION: This genus differs from *Nematobothrium* van Beneden in the following points: (1) free in host tissue; (2) ceca provided with well-developed gland cells at the beginning, terminating at posterior extremity; (3) testes paired, extending from behind genital junction to near anterior extremity; (4) ovary extending in testicular region; (5) uterus descending to posterior extremity where it takes its final ascending course.

#### *Nematobothrioides* n. gen.

GENERIC DIAGNOSIS: Didymozoidae, Nematobothriinae. Complete hermaphrodite free in host tissue. Body narrow, long, almost uniformly wide. Oral sucker larger than pharynx. Posterior end of esophagus and anteriormost portion of ceca surrounded by prominent glandular cells, ceca terminating at posterior end of body. Acetabulum absent. Testes juxtaposed. Genital pore ventral, close to pharynx. Ovary and vitellarium single, tubular, long, winding; former confined to testicular region, latter between ovary and posterior extremity. Uterus first descending to posterior extremity where it takes its final ascending course. Parasitic in subcutaneous connective tissue of marine teleosts.

TYPE SPECIES: *N. kalikali* n. sp., in subcutaneous connective tissue of opercular region of *Pristipomoides sieboldii*; Hawaii.

#### 13. *Neonematobothrium kawakawa*

n. gen., n. sp.

Fig. 13 A–E

HABITAT: Free in subcutaneous tissue of opercular region of *Euthynnus yaito* (local name "kawakawa"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S.Y. No. 31.

DESCRIPTION (based on three whole mounts): Body flattened, slender, 32–48 mm long by 0.07–0.65 mm wide (about 37 mm long by 70  $\mu$  wide in the type), tapered anteriorly to a sharp point, but rounded at posterior extremity. Cuticle smooth throughout. Oral sucker and pharynx rudimentary, 10–23  $\mu$  and 7–14  $\mu$  wide respectively. Esophagus simple and slender anteriorly, but profusely diverticulate on each side and surrounded by numerous small glandular cells for its greater posterior part, bifurcating in the type at a distance of 16.7 mm from head end into two limbs of similar structure and of unequal length; each limb is continued backward into a strongly twisted, narrow, tubular cecum, which terminates near the posterior extremity. No acetabulum.

Testes two, narrow, strongly twisted, parallel to each other for the most part, but originating at different levels; posterior testis originating 0.5 mm from tail end and anterior testis arising 12.5 mm further anteriorly in the type; each passing imperceptibly into vas efferens. In the type one vas efferens is swollen (50  $\mu$  across) before joining its fellow at a distance of 5.5 mm behind anterior end of ovary, 8.8 mm from head end. Vas deferens winding forward in median field close to final ascending limb of uterus. Common genital pore almost midventral, shortly behind pharynx.

Ovary narrow, twisted like testes, originating 2.0–3.7 mm posterior to head end just at the level where the proximal ascending uterus crosses the median line from the left to the right as in the type, or 1.1–2.4 mm further behind this level. It extends backward in the type for about 17 mm, turning from side to side several times, terminating at a distance of 20.5 mm from anterior extremity, where it joins the anterior end of the ascending vitellarium. This genital junction is, therefore, posterior to the midbody in the type as well as in one speci-

men 32 mm long, but in the longest specimens (48 mm) it lies anterior to the midbody dividing the body in ratio of 21:27. Seminal receptacle oval,  $100 \times 80 \mu$  in the type, situated dorsal to this point of genital junction. Descending uterine duct surrounded by shell gland for a length of about 0.4 mm in the type, turning forward in the type across median line from one side to the other at a distance of 0.9 mm from posterior extremity; this ascending uterine limb turns across the median line once more 3.3 mm posterior to the head end to take an exactly identical descending course on the opposite side and passes into the final ascending limb 0.55 mm from the posterior extremity; thus the entire uterus forms three loops, one at a short distance from the head end and two near the posterior extremity; distal portion of final ascending uterine limb differentiated into muscular metraterm which runs forward nearly in the median field along with the vas deferens; eggs bean-shaped,  $14\text{--}21 \times 7.5\text{--}12 \mu$ . Vitellarium narrow, tubular, strongly twisted throughout. In the type it originates 0.2 mm from posterior end of body and runs forward medial to proximal ascending uterine limb opposite testes. Excretory vesicle tubular, somewhat winding in median field, its anterior termination not made out; excretory pore terminal.

**DISCUSSION:** This genus bears a certain resemblance to *Allometanematobothrioides*, especially in that the uterus makes three U-turns (though turning first near the posterior extremity instead of posterior to the ovary), and in the intestinal limbs being very narrow and very strongly convoluted, and in the anterior extremity markedly tapering. But the two genera differ fundamentally in the structure of the esophagus.

*Neonematobothrium* n. gen.

**GENERIC DIAGNOSIS:** Didymozoidae, Nematobothriinae. Body long, slender, flattened, markedly tapered anteriorly. Oral sucker and pharynx rudimentary. Esophagus unusually long, with numerous diverticles surrounded by gland-

ular cells, bifurcating in midregion of body into unequal branches, each of which passes into a very narrow, convoluted cecum terminating near posterior extremity. Acetabulum absent. Testes narrow, twisted, parallel to each other for the most part, originating at different levels; posterior testis largely in greater posterior portion of body. Genital pore ventral, postpharyngeal. Ovary single, tubular unbranched, originating at level of anterior U-turn of uterus or further behind it. Seminal receptacle present. Uterus first descending to near posterior extremity, then ascending and turning backward a short distance back of anterior extremity, forming another U-turn near posterior extremity before taking its final ascending course; eggs bean-shaped, small. Vitellarium single, narrow, tubular, extending between ovary and posterior extremity. Excretory vesicle with terminal pore, probably bifurcating anteriorly. Parasitic, free in subcutaneous tissues of opercular region of marine teleosts.

**TYPE SPECIES:** *N. kawakawa* n. sp., in *Euthynnus yaito*; Hawaii.

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## Contribution to the Marine Chlorophyta of Hawaii, II Additional Records<sup>1</sup>

WILLIAM J. GILBERT

THE ANNOTATED LIST which follows is comprised mostly of new or previously unreported marine green algae from the Hawaiian Islands. Sources of material studied are listed in an earlier paper (Gilbert, 1962) with the exception of a few incidental collections forwarded to me during recent months by Dr. Maxwell S. Doty.

This nearly completes a survey of the marine Chlorophyta of this area which was initiated in 1959 by a four-month visit to the islands. The writer has still some material that is not named, particularly of *Enteromorpha* and *Cladophora*, and only species in these genera are listed for which there seems to be reasonable certainty at this time.

The following species constitute new records for the Hawaiian Islands: *Enteromorpha clathrata* (Roth) Greville, *E. plumosa* Kützinger, *Monostroma oxyspermum* (Kützinger) Doty, *Ulva expansa* (Setchell) Setchell and Gardner, *U. reticulata* f. *delicatula* n. f., *Chaetomorpha brachygonia* Harvey, *C. gracilis* Kützinger, *C. indica* Kützinger, *C. paucitatis* n. sp., *Rhizoclonium grande* Børgesen, *R. bookeri* Kützinger, *R. riparium* (Roth) Harvey, *Cladophora dotyana* n. sp., *C. hemisphaerica* Gardner, *Boodleopsis hawaiiensis* n. sp., *Codium saccatum* Okamura.

Type material is deposited at the University of Michigan Herbarium, Ann Arbor.

1. *Enteromorpha clathrata* (Roth) Greville, 1830, p. 181.

In both collections the plants are slender throughout and have many narrow branches some of which end in a uniseriate row of cells. The arrangement of cells in longitudinal rows throughout the plants and the presence of 3–5

pyrenoids in each cell confirm the plants as being *E. clathrata*.

COLLECTIONS: *Gilbert* 9379, entangled on other algae, Ala Moana Park, Honolulu, Oahu, April 7, 1959; 9969, in wash of little bay at Milolii, Hawaii, May 30, 1959.

2. *Enteromorpha flexuosa* (Wulfen) J. Agardh, 1883, p. 126.

COLLECTIONS: *Gilbert* 9016, Waikiki, Honolulu, Oahu, March 11, 1959; 9286, ½ mile E of McGregor's Pt., Maui, March 25, 1959; 9542, growing on basalt near high tide line, Wailua, Kauai, April 25, 1959; 9576, attached to rocks in active sand in from 1–3 feet of water at low tide level, Anahola, Kauai, April 26, 1959; 9922, from rocks which were slightly covered with sand, submerged at high tide, and frequently washed by wave action at low tide, Hookena, Hawaii, May 25, 1959; 10061, from rocks on shore between low and high tide levels, between Kawela and Kamaloo, Molokai, June 5, 1959.

3. *Enteromorpha intestinalis* (L.) Link, 1820, p. 5.

COLLECTIONS: *Gilbert* 9175, Camp 1, Sprecklesville, Maui, March 23, 1959; 9382, canal at River St., near Nimitz Highway, Honolulu, Oahu, April 7, 1959.

4. *Enteromorpha lingulata* J. Agardh, 1883, p. 143.

COLLECTION: *Gilbert* 9507, attached to rocks covered with a shallow layer of active sand, Haleiwa Park, Oahu, April 18, 1959; 9729, on basalt and coral rocks, Anahola, Kauai, May 2, 1959.

5. *Enteromorpha plumosa* Kützinger, 1843, p. 300, pl. 20, fig. 1.

COLLECTION: *Gilbert* 9027, scraped from walls of tide pool filled with recurring waves, Diamond Head, Oahu, March 14, 1959.

<sup>1</sup> Albion College, Albion, Michigan. This study was supported by two grants from the National Science Foundation (NSF G7107 and NSF G25137). Manuscript received May 8, 1963.

6. *Enteromorpha ?tubulosa* Kützing, 1856. Tab. Phyc. VI, p. 11, pl. 32, fig. 2.

The following collection is assigned to this species with considerable uncertainty, especially since the cells appear to have 1–3 pyrenoids instead of but one as usually noted in the literature.

COLLECTION: *Gilbert* 9705, attached to clay tile at Kauai Boat Club between Kekaha and Waimea, Kauai, April 30, 1959.

7. *Monostroma oxyspermum* (Kützing) Doty, 1947, p. 12.

All of the collections listed below appear to be one species. Surface views and cross section studies were made. The average cell diameter is almost the same (about  $9\ \mu$ ) in all collections and the thalli (with the exception of *Gilbert* 9377) are all about 20–25  $\mu$  thick. Cells were grouped in twos, threes, and fours in surface view and all appeared somewhat taller than wide in cross sectional view, the thickness of the membrane external to the cells contributing mostly to the variation in thickness of the frond.

COLLECTIONS: *Gilbert* 9377, on cement wall at high tide level in canal, Ala Moana Park, Honolulu, Oahu, April 7, 1959; 9481, wall of Natatorium, Waikiki, Honolulu, Oahu, April 15, 1959; 9785, in quiet water around mangrove roots near docking area, Coconut Island, Kaneohe Bay, Oahu, May 14, 1959; *Meñez* 722, from basalt rocks covered with thin film of mud, above high tide line, in back of YWCA camp, Kaneohe Bay, Oahu, (no date); *Doty* 17204, highest tidal rocks in pool at Coconut Island, Hilo, Hawaii, Dec. 28, 1958; *Bernatowicz*, A. J. (no number), on stones where Kuliouou stream debouches into Maunalua Bay, Oahu, April 8, 1956.

8. *Ulva expansa* (Setchell) Setchell and Gardner, 1920, p. 284.

This relatively common *Ulva* is characterized by having broad unbranched thalli with ruffled margins and in having the thalli thicker in the middle than at the margins. Thalli of the Hawaiian material reach 30 cm in width and 43 cm in length, and range in thickness from 40–70  $\mu$  near the margin and from 75–100  $\mu$  in the center. Collections were made of attached

material from cement or rocks in the intertidal zone and of free-floating material in quiet tide pools.

COLLECTIONS: *Gilbert* 9131, Kahana, West Maui, March 22, 1959; 9520, forming a distinct zone at high tide level on cement wall of pier running out from Natatorium-end of Kuhio Beach, Waikiki, Honolulu, Oahu, April 22, 1959; 9636, in tide pool at Port Allen, Kauai, near Salt Pond Beach, April 27, 1959; 9933, from tide pool at Honaunau, Hawaii, May 26, 1959; 9978, from rocks, intertidal zone, 1.5 miles S of Kailua, Hawaii, May 31, 1959.

9. *Ulva fasciata* Delile, 1813, p. 153, pl. 58, fig. 5.

This is a common species, previously reported from Hawaii by several authors. It is extremely variable in form. Only a few of the collections studied are listed.

COLLECTIONS: *Gilbert* 9218, 9219, Hookipa Park, West Maui, March 24, 1959; 9356, Hauula Park, Oahu, April 4, 1959; 9635, low tide level in active surf, near Salt Pond, Port Allen, Kauai, April 28, 1959; 9709, on rocks of breakwater, Nawiliwili Boat Harbor, Kauai, April 30, 1959; 9921, in 1–3 feet of water, attached to rocks, Hookena, Hawaii, May 25, 1959; 10116, rocks in quiet water, Mapalehu, Molokai, June 7, 1959.

10. *Ulva lactuca* Linnaeus, 1753, p. 1163.

COLLECTIONS: *Gilbert* 9380, in canal on River Street, near Nimitz Highway, Honolulu, Oahu, April 7, 1959; 9386, on reef flat at Ala Moana Park, Honolulu, Oahu, April 8, 1959; 9548, on reef at Wailua, Kauai, April 25, 1959; 10065, attached to iron plates of tug boat, Kaulakakai, Molokai, June 6, 1959.

11. *Ulva reticulata* f. *delicatula* f. n.

Fig. 1

Frons non affixa, in algis aliis implicata, segmentis angustis reticulatisque, telis multis parvisque, frons ita delicata videtur; frons 32–36  $\mu$  crass, cellulae in duobus stratis, 7–13  $\mu$  diam a superficie visae, a sectione transversa visae fere rotundae, in matrice gelatinosa laxae dispositae.

*Gilbert* 9947, TYPUS, e loco Kahaluu Park ad Kailua, Hawaii dicto, m. May 26, 1959 lectus.

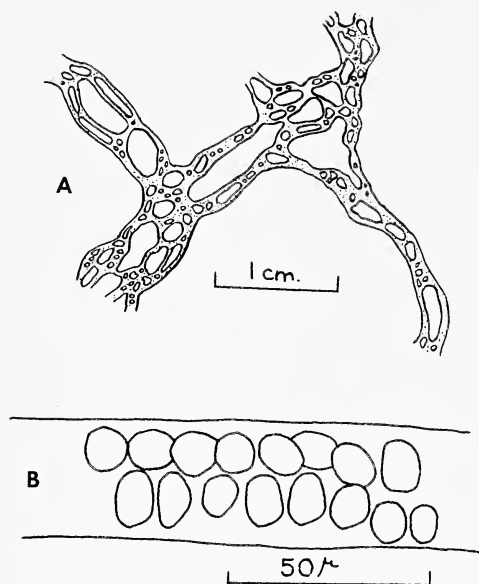


FIG. 1. *Ulva reticulata* f. *delicatula* f. n. A, Habit sketch of small portion of frond; B, transverse section of frond showing cell outlines.

Frond entangled in other algae, apparently unattached, its segments narrow and reticulate, the meshes numerous and small, thus giving the frond a delicate appearance; frond  $32\text{--}36\ \mu$  thick, cells in two layers,  $7\ (10\text{--}11)\text{--}13\ \mu$  diam in surface view, nearly round in cross sectional view, loosely arranged in the gelatinous matrix.

COLLECTION: *Gilbert* 9947, TYPE, Kahaluu Park, S of Kailua, Hawaii, May 26, 1959.

This collection was first reported by the writer (1962:143) as *Ulva reticulata* Forsskål (1775:187) but later study suggested it is sufficiently different to be regarded as a form of that species. It differs from forma *reticulata* in its much more delicate appearance resulting from the extremely fine meshes, in the fact that the frond is thinner ( $32\text{--}36\ \mu$ , as compared with the usual  $50\text{--}76\ \mu$ ), and in that the cells are less closely arranged and at most only slightly elongated when viewed in a cross section of the frond.

## 12. *Ulva rigida* C. Agardh, 1822, p. 410.

The following collection is assigned with some uncertainty to this species. Only two fronds were found in a large mound of algae washed up on the beach by wind and wave action. One frond was a very dark green and

both were relatively stiff and leathery, certainly different to the touch from other *Ulva* in the pile. The two fronds are ovate, about 11 cm in length with a distinct but very short petiole. The fronds reach  $137\ \mu$  in thickness. When seen in a cross section of the frond the cells are vertically elongated, up to 4 times their width in length, and the gelatinous matrix between and external to the cell layers is wide.

COLLECTION: *Gilbert* 9188, in wash at Naska, Maui, March 23, 1959.

## 13. *Chaetomorpha antennina* (Bory) Kützting, 1849, p. 379.

This species commonly occurs where exposed to surf and actively moving water as in spillways. Rather large quantities of material have been examined with particular reference to the basal cell and considerable variation in basal cell size and degree of annulation have been noted. For example, in plants which appear to belong to the same clone (of *Gilbert* 9761) there are a few apparently mature plants with basal cells having no annulations, but in most plants the annulations are distinct and numerous. This species has been reported previously by several authors and only representative collections of my own are reported.

COLLECTIONS: *Gilbert* 9141, Kalama Park, Maui, March 23, 1959; 9417, near Kahe Point, Oahu, April 11, 1959; 9761, base of Na Pali Cliffs, near Mana, Kauai, May 3, 1959; 9839, Onekahakaha Beach, Hilo, Hawaii, May 22, 1959; 10079, ca. 3 miles N of Wailua, Molokai, June 6, 1959.

## 14. *Chaetomorpha paucitatis* sp. n.

Fig. 2

Plantae non crebrae, dilute virides,  $4.5\text{--}5\ \text{cm}$  alt., metallicae rigidaeque, parte in inferiore laxae  $2\text{--}3$  convolutae, in penicillis  $2\text{--}5$  plantarum singularum; cellulae basales  $200\text{--}700\ \mu$  long.,  $57\text{--}130\ \mu$  lat., longioribus a crescentia rhizoideorum secundariarum, quae e cellulis supra in cellulam basalem primariam, hapteron discoidium habentem, descendunt, orientibus; cellulae in filamento inferiore  $150\text{--}190\ \mu$  diam, ad septa interdum constrictae supra maiora (ad  $500\ \mu$ ) factae, et per formationem zoosporarum inflatae; membrana cellularum striata, crassitudine vari-

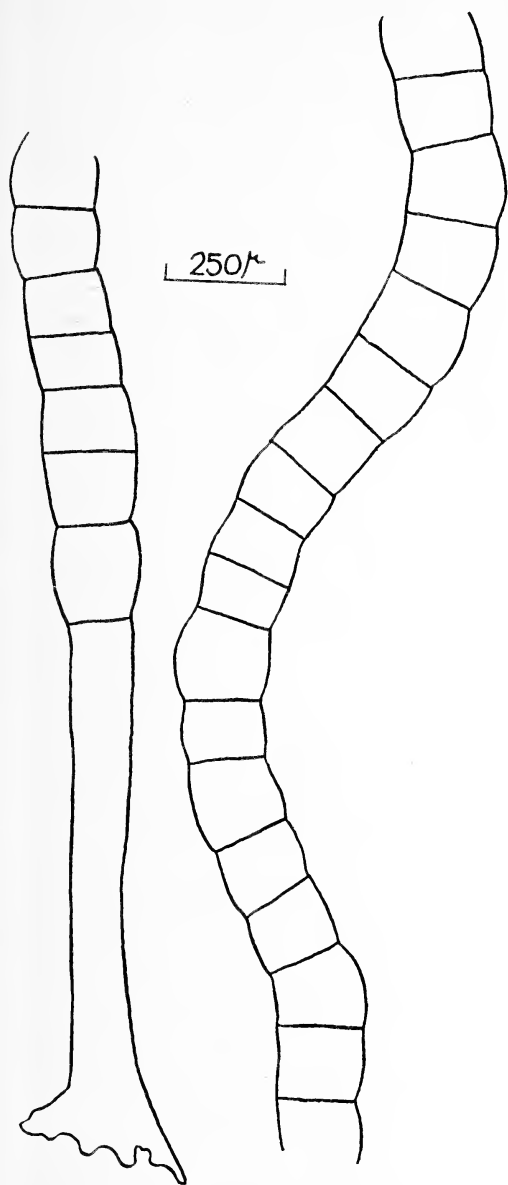


FIG. 2. *Chaetomorpha paucitatis* sp. n. Basal cell and portion of the filament immediately above a basal cell showing one of the spirals.

ans, in cellulis basalibus usque ad  $18\ \mu$ , in cellulis aliis usque ad  $14\ \mu$ .

*Gilbert 9521*, TYPUS, in superficie horizontali massarum "concreti" in aqua non profunda e loco Kuhio Beach, Waikiki, Honolulu, Oahu dicto, m. April 22, 1959 lectus.

Plants uncrowded, light green, 4.5–5 cm tall, in tufts of 2–5, wiry and stiff to touch, laxly spiralled 2–3 times in lower part; basal cells 200–700  $\mu$  long, 57–130  $\mu$  wide, the longer ones derived from the growth of secondary rhizoids into the primary basal cell which has a disk-like holdfast; cells in lower filament 150–190  $\mu$  diam, occasionally constricted at septa, becoming larger above (to 500  $\mu$ ) and inflated during zoospore formation; cell walls striated, thickness variable, up to 18  $\mu$  in basal cells and to 14  $\mu$  in other cells.

COLLECTIONS: *Gilbert 9521*, TYPE, growing on horizontal surface of cement blocks in shallow water, Kuhio Beach, Waikiki, Honolulu, Hawaii, April 22, 1959; 9799, same location, May 16, 1959.

The plants described here as new are most suggestive of *Chaetomorpha aerea* (Dillwyn) Kützing, differing from that species in its lighter color and in the fact that only a few plants arise in a tuft instead of being strongly gregarious.

15. *Chaetomorpha brachygona* Harvey, 1858, Ner. Bor.-Amer., pt. 3, p. 87, pl. 46A, fig. 1, 2.

COLLECTIONS: *Gilbert 9927*, from muddy water, 1–3 feet below surface in a little bay, Honaunau, Hawaii, May 26, 1959; *Doty 12383A* (in part), washed in at beach laboratory, Waikiki, Honolulu, Oahu, Feb. 6, 1958.

16. *Chaetomorpha gracilis* Kützing, 1845, p. 203.

COLLECTIONS: *Doty 12440*, in large soft "pillow" on very fine sand on bottom of hole in reef (–4 ft) at Hanauma Bay, Oahu, April 6, 1954; 12650, forming skein of relatively untangled filaments over a "room-size" area in Waikiki Natatorium in about 10 ft of water on sandy mud bottom, Waikiki, Honolulu, Oahu, Sept. 25, 1954.

17. *Chaetomorpha indica* Kützing (prox.), 1849, p. 376.

Assignment of the collections below to *C. indica* is made with considerable uncertainty.

COLLECTIONS: *Gilbert 9348*, 9349, entangled on other algae, two to four feet below the surface, Hauula Park, Oahu, April 2, 1959.



18. *Rhizoclonium grande* Børgesen, 1935, p. 14, figs. 5–6.

Fig. 4, E

This large *Rhizoclonium* was found growing most frequently on flat rock surfaces and nearly covered with a thin layer of sand which was probably trapped by the interwoven filaments. Filaments of the Hawaiian material range from 225–400  $\mu$  in diameter, with the cells from three-fourths to three diameters long. I have compared the Hawaiian plants with those of a collection from Mauritius (*Morin 1151*) identified by Børgesen as *R. grande* and found the plants in both collections to agree closely.

COLLECTIONS: *Gilbert 9509*, abundant on rock flats especially where covered with thin layer of sand, Kaena Pt., Oahu, April 18, 1959; 9660, Anahola Beach, Kauai, April 29, 1959; 9945, on rocks covered with thin layer of sand, Kahaluu Park, Hawaii, May 26, 1959; 10003, Honaunau Beach, Hawaii, June 1, 1959.

19. *Rhizoclonium hookeri* Kützinger, 1849, p. 383.

COLLECTIONS: *Doty 13291*, present in gas holes and small cracks of solid rock about 2.5 ft above high tide line at 115 East Banyan Drive, Hilo, Hawaii, Aug. 16, 1956; *Setchell 5220*, Coconut Island, Hilo, Hawaii, July 14, 1900\*.

20. *Rhizoclonium riparium* (Roth) Harvey, 1849, p. 238.

COLLECTIONS: *Gilbert 9962*, in wading pool on Coconut Island, Hilo, Hawaii, May 27, 1959; *Doty 8671*, large mass stuck in a coral head, Hauula Bay, Oahu, Feb. 24, 1951; 8248, near mouth of Manini Gulch, Kauna, Oahu, Oct. 21, 1950.

21. *Cladophora dotyana* sp. n.<sup>2</sup>

Fig. 3

Plantae sparsae aut in tegetibus gregariae,

<sup>2</sup> Since this manuscript was accepted for publication *Cladophora patula* Sakai has been described as new and appears to be the same species (pp. 22–25 of Y. Sakai, 1964). The species of *Cladophora* from Japan and its vicinity, Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University 5(1):1–104, 17 pls.

fusco-virides, 2–4 cm alt., rudes rigidaeque, per extensiones rhizoidales 2–4 cellularum infimarum relative brevium affixae; cellulae admodum super basales 3.5–12 mm long., ad 600  $\mu$  lat., ad extremitates distales 3–4 (raro 5) ramos efficientes, ramis saepe late divaricatis ad retrorsos, interdum contortis, ex una cellula sola ad hanc altitudinem plerumque constantibus, ramificatio supra plerumque di-trichotoma, ramis multis erectisque, cellulis, ut filamenta fruticulosa velut per ventum defflexa videantur, saepe in eadam directione curvatis, cellulis 1.2–4 diam long., 210–300  $\mu$  lat., septis inter ramos crebris, cacumina ramorum obtusa; cellulae per plantam cylindricae, non inflatae, membranis striatis, in cellulis inferioribus 25  $\mu$  (15–37  $\mu$ ) crass, in cellulis superioribus 12  $\mu$  (7.2–18  $\mu$ ) crass.

*Gilbert 9214*, TYPUS, in superficie inferiore rupis lacui minuente aestu imminens, in loco Hookipa Park, East Maui dicto, m. March 24, 1959 lectus.

Plants sparse or in gregarious mats, dark green, 2–4 cm high, coarse and stiff, attached by rhizoidal extensions of the 2–4 lowermost relatively short cells; cells immediately above the basal cells 3.5–12 mm long to 600  $\mu$  wide, giving rise to 3–4 (rarely 5) branches at their distal ends, the branches frequently widely divaricate to retrorse, at times contorted, and usually consisting of but one cell at this level; above branching usually di-trichotomous, numerous, the branches erect with cells often curving in one direction to give a wind-blown appearance to the tufted filaments, the cells 1.2–4 diameters long, 210–300  $\mu$  wide, with septa frequent between branches; branch tips obtuse-rounded; cells cylindrical throughout the plant, not inflated, their walls striated, 26  $\mu$  (15–37  $\mu$ ) thick in lower cells, 12  $\mu$  (7.2–18  $\mu$ ) in upper cells.

COLLECTION: *Gilbert 9214*, TYPE, on the under surface of a rocky overhang in tide pool, Hookipa Park, East Maui, Hawaiian Islands, March 24, 1959.

This unusual and distinctive *Cladophora* bears little resemblance to other robust species. It is characterized by its short stature,

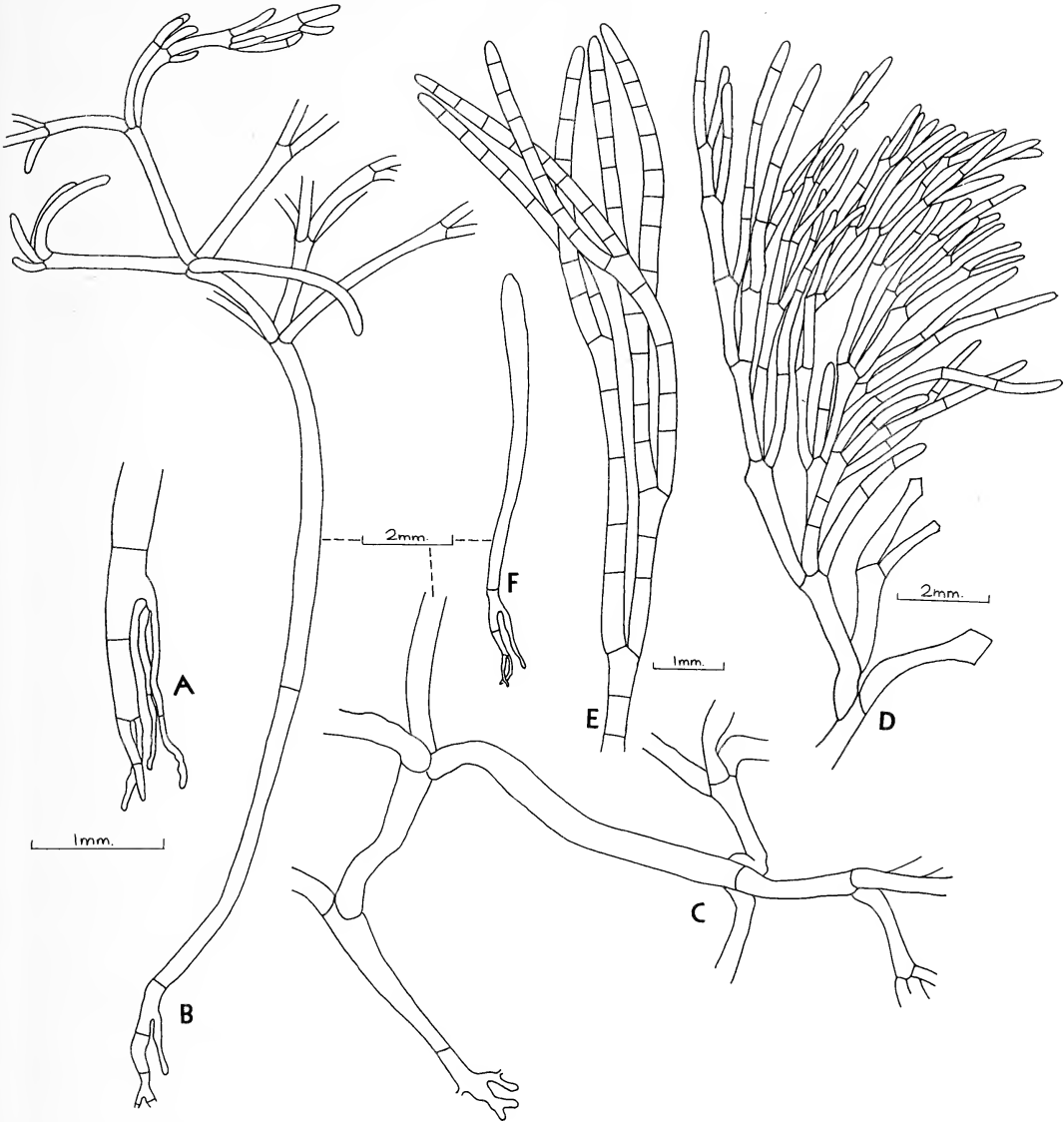


FIG. 3. *Cladophora dotyana* sp. n. A, Basal cells; B, a nearly complete young plant; C, portion of the lower part of a mature plant; D, E, terminal portions of a mature plant; F, a very young plant.

wind-blown appearance, large diameter stiff filaments, extremely long primary cells, and frequent widely divaricate to retrorse condition of the primary branches. None of the plants in several collections has exceeded 4 cm in height even though growth appeared to be luxurious. It differs from *C. fuliginosa* Kützing in that branching in *C. dotyana* is often tri- or quadrichotomous in the lower two-thirds of

the plant, the upper cells are not strongly arcuate, and the tip cells are relatively much shorter for their diameter than in the former species. Perhaps *C. dotyana* most closely resembles *C. prolifera* (Roth) Kützing and *C. pellucida* (Huds.) Kützing. *C. dotyana* is much shorter, more closely branched, and lacks the fasciculate grouping of the ultimate branchlets of *C. pellucida*. Furthermore, the proposed species does

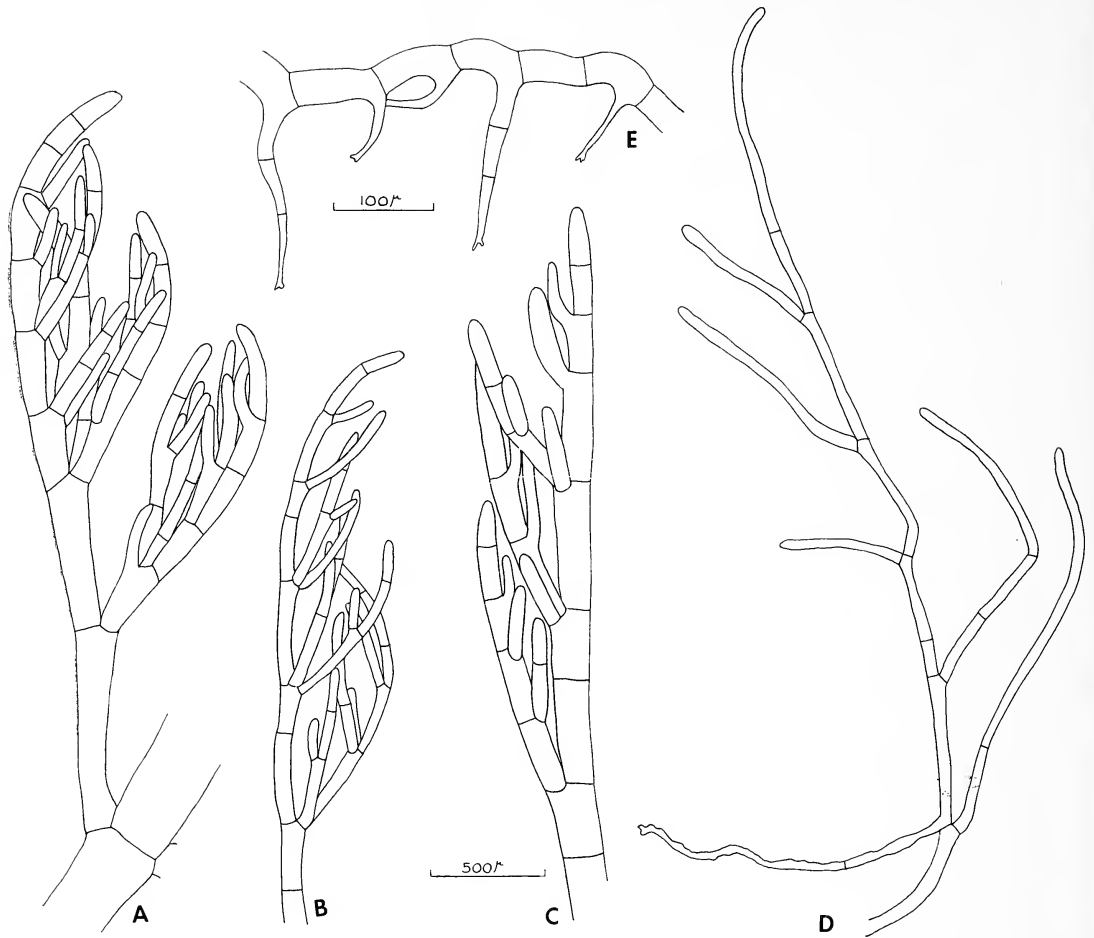


FIG. 4. A, B, *Cladophora inserta* f. *ungulata* (Brand) Setchell. A, Terminal cluster of branches in the size-range of *C. fascicularis*; B, terminal branch cluster of *C. inserta* f. *ungulata* of usual size range; C, *C. fascicularis* (Mertens) Kützing, terminal branch cluster; D, *C. socialis* var. *hawaiiiana* Brand, habit sketch; E, *Rhizoclonium grande* Børgesen, short section of a filament.

not have the unusually long lower cells so characteristic of *C. pellucida*. It can be separated from *C. prolifera* by the fact that all branches of *C. prolifera* seem to be erect, showing no tendency toward the widely divergent to retrorse branching in the lower part of the frond of *C. dotyana*. *C. radiosa* (Suhr) Kützing, *C. wrightiana* Harvey, and *C. valonioides* Sonder are three additional species having wide diameter filaments, but none of these bears resemblance to *C. dotyana*.

It is of interest to note that in the Herbarium of the University of California there are three collections of this proposed species which were

made in Hawaii. All three collections were made in the early part of the century by Miss Minnie Reed and are filed under the name of *Cladophora valonioides* Sonder. These specimens bear Miss Reed's numbers 149, 386, and 1160, and the collections were made on Maui, Kauai, and Oahu, respectively.

OTHER COLLECTIONS: Gilbert 9036, in crevice at end of Laie Pt., Oahu, March 17, 1959; 9046, at low tide level in crevices and occasionally on exposed surfaces in basalt dike, Hanauma Bay, Oahu, March 19, 1959; 9228, between Hookipa Park and Paia, Maui, March 24, 1959; 9818, Kapaa Park, near Mahukona Har-

bor, Hawaii, May 21, 1959; 9991, Palemano Pt., at S end of Kealakekua Bay, Hawaii, June 1, 1959; 10128, ca. 3 miles NE of Wailua, Molokai, June 7, 1959.

22. *Cladophora fascicularis* (Mertens) Kützing, 1843, p. 268.

This species is relatively common and is frequently found attached or free-floating in the wash along the shore. In its typical form (Fig. 4, C) it is easily distinguishable from *C. inserta* f. *ungulata* (Brand) Setchell, but there are many intermediates to suggest that the two species may be the same, as suggested by Børgesen (1948:8) who still listed them separately. Certainly the extremes are readily recognizable.

COLLECTIONS: Gilbert 9126, Kahana, Maui, March 22, 1959; 9171, Camp 1, Sprecklesville, Maui, March 23, 1959; 9189, Naska, Maui, March 23, 1959; 9297, Maalaea Boat Harbor, Maui, March 25, 1959; 9708, Nawiliwili Boat Harbor, Kauai, April 30, 1959.

23. *Cladophora hemisphaerica* Gardner, in Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 2240 (nomen nudum), in Collins, F. S., 1918, p. 83 (descr.).

These plants rather closely follow Gardner's description. They were more or less crowded on a horizontal rock surface and appear as dense, hemispherical, dark green tufts, 1–2 cm in diameter. The lower branches have cells to 65–70  $\mu$  diam, 1–3 diam long, and the branches are widely divergent. Branchlets in outer part of the thallus have cells to 45–70  $\mu$  diam, with the branches less divergent.

COLLECTION: Gilbert 9946, on horizontal rock surface washed by waves, Kahaluu Park, Hawaii, May 26, 1959.

24. *Cladophora inserta* f. *ungulata* (Brand) Setchell, 1926, p. 75, pl. 22.

In its typical form (Fig. 4, B) this plant is easily separated from *C. fascicularis* on the basis of the much smaller diameter of the ultimate segments and the characteristic curving of the terminal branchlets. Figure 4, A was drawn from a collection containing plants which, while maintaining the curved aspect of the terminal branchlets, are as large as *C. fascicularis*.

Hawaii is the type locality for this form of *C. inserta*. It was first described by Brand (1905, p. 180, pl. 5, figs. 10, 11) as *C. mauritiana* var. *ungulata* from material collected by Tilden.

COLLECTIONS: Gilbert 9010, between Elks' Club and Natatorium, Waikiki, Honolulu, Oahu, March 11, 1959; 9022, in wash, Waikiki, Honolulu, Oahu, March 14, 1959; 9148 and 9149, Kalama Park, Maui, March 23, 1959; 9373, in shallow water, near shore, near Laie Pt., Oahu, April 4, 1959; 9479, on Natatorium wall, Waikiki, Honolulu, Oahu, April 15, 1959.

25. *Cladophora socialis* var. *hawaiiiana* Brand, 1905, p. 182.

This species (Fig. 4, D) is common in warm, shallow tide pools as soft, oval, greyish-green, spongy masses. It is a species having wide distribution.

COLLECTIONS: Gilbert 9052, on sides of tide pools on bench of old lava flow where washed by high waves, Hanauma Bay, Oahu, March 19, 1959; 9230, between Hookipa Park and Paia, Maui, March 24, 1959; 9535, from tide pool at Spouting Horn, Kauai, April 24, 1959; 9741, from pools in basalt rock at Poipu Beach Park, Kauai, May 2, 1959; 9815, from tide pools in lava, Kapaa Park, Hawaii, May 21, 1959; 10083, 3 miles NE of Wailua, Molokai, June 6, 1959.

26. *Boodleopsis hawaiiensis* sp. n.

Fig. 5

Planta parva siphonacea viridis, pulvillos coarctos in arena in rimis umbrosis fossarum laevae 7–10 metra super aquae altitudinem aestu alto efficiens; filamenta inferiora (obtecta) aliquantulum laxa, (plerumque) dichotome ramosa, sine constrictionibus ad bases ramorum, pauciores chloroplastos quam in parte plantae superiore habentia, diametro varians, ab 11–60  $\mu$ , membranis crassitudine variantibus, saepe striatis; nonnulli rami inferiores descendentes, satis tenues, fere sine colore, aspectu rhizoidei facti, rami rhizoidei, autem, ubilibet in planta saepe reperti; filamenta superiora diametro uniformiora, 16–23 (30)  $\mu$  lat., chloroplastis parvis rotundis ad ovatos, ut videtur sine pyrenoidis, conferte impleta, ramificatio dichotoma ad manifeste lateralem, constrictionibus ad bases ramorum manifestis; constrictiones secundaria inter ramos sparsae aut nullae.

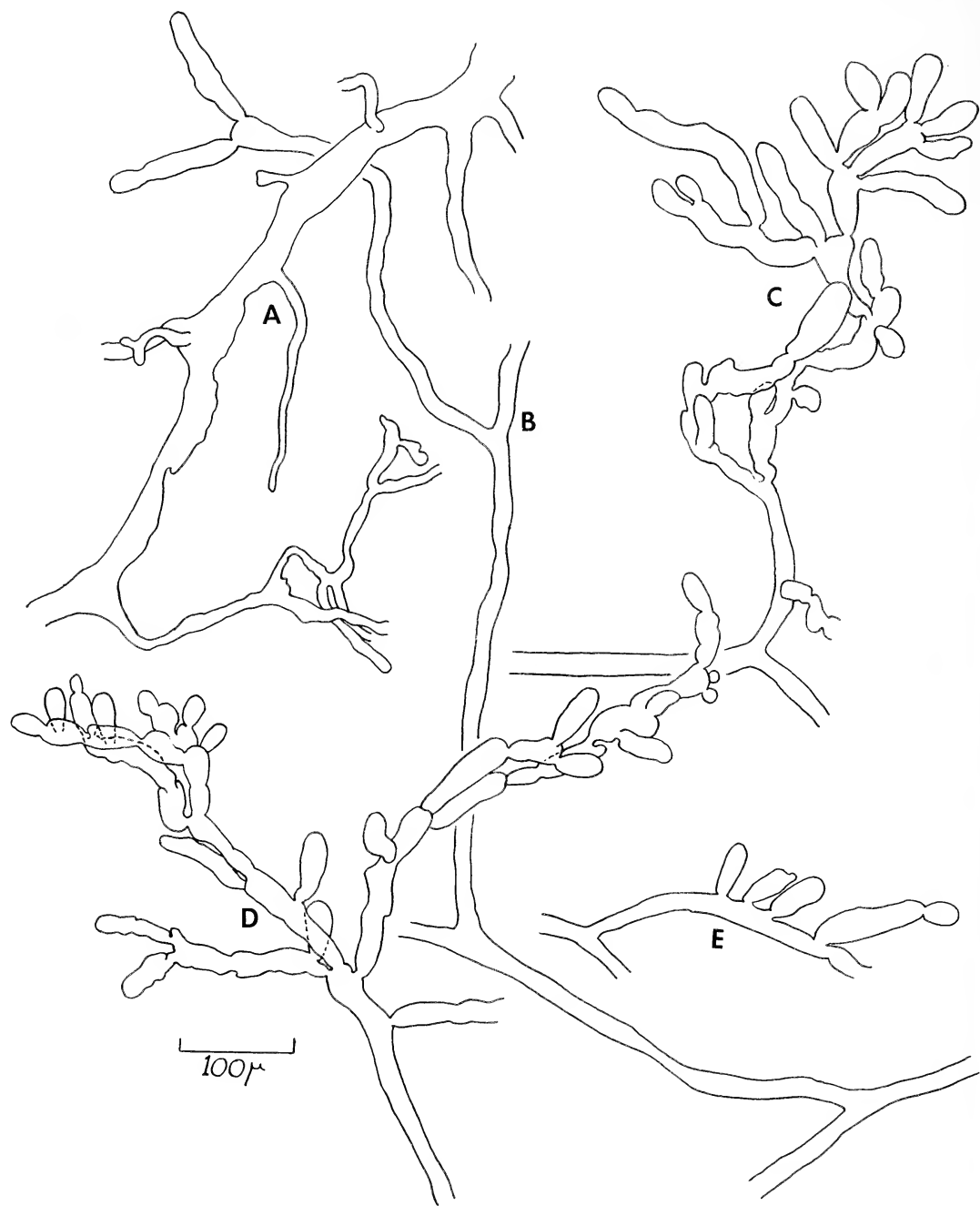


FIG. 5. *Boodleopsis hawaiiensis* sp. n. A, Portion of lower covered filaments; B, appearance of other lower filaments with remote dichotomies lacking constrictions (there is a terminal or upper part to this figure which shows a dichotomy with constrictions); D, E, upper branchlets showing lateral to di-trichotomous branching and the constrictions which are largely confined to branch bases just above the dichotomies.

*Doty 19255*, TYPUS, super fossam lavae prae-historicam 6–8 metra super arenam atque aquae altitudinem aestu alto, ca. 17 metra versus orientem fluminis lavae 1955 Keekee in loco Puna, Hawaii dicto, m. Dec. 23, 1959 lectus.

Plant small and siphonous, green, forming felted cushions on sand in shaded crevices of lava dikes 20–30 ft above high tide line; lower (covered) filaments somewhat lax, (usually) dichotomously branched with no constrictions at branch bases, and with fewer chloroplasts than in upper part of plant, diameter variable, from 11–60  $\mu$  and with walls of variable thickness and often striated; some of lower branches descending, becoming quite slender, almost colorless, and rhizoidal in appearance, but rhizoidal branches may, and often do, occur at almost any part of the plant; upper filaments more uniform in diameter, 16–25 (30)  $\mu$ , crowded with small round to oval chloroplasts that are apparently without pyrenoids, branching di-trichotomous to distinctly lateral with constrictions evident at branch bases; secondary constrictions between branches infrequent to absent.

COLLECTIONS: *Doty 19255*, TYPE, on top of prehistoric lava dike, 6–8 meters above the sand and high tide line, about 50 ft E of the 1955 Keekee lava flow, Puna, Hawaii, Dec. 23, 1959; 19355, growing in shaded crevices about 20–30 ft above high tide line about ¼ mile E of the 1955 lava flow in Keekee, Puna, Hawaii, Sept. 8, 1960.

After a prolonged study I have come to the conclusion that the material represents an undescribed species of *Boodleopsis*, which itself is a rather uncertain genus<sup>3</sup> in the Siphonales.

*Boodleopsis* was established by A. and E. S. Gepp (1911:64) who named and described *Boodleopsis siphonacea*. Subsequently two species have been added to the genus, *B. pusilla* (Collins) Taylor, Joly, and Bernatowicz (by transfer from *Dichotomosiphon*) and *B. verticillata* Dawson (1960:32). The proposed species differs from *B. siphonacea* and *B. pusilla* in its smaller size, the fact that it lacks the secondary constrictions between the branches of its upper filaments, and in that it frequently

branches laterally, sometimes to the exclusion of di- or trichotomous branching. *B. hawaiiensis* differs from *B. verticillata* in its distinctly smaller size and the lack of verticillate branching. Attention should also be called to the fact that all three of the previously described species are known from a muddy substratum on reefs or in estuaries, while *B. hawaiiensis* was found on a sandy substratum in shaded crevices of a lava dike 20–30 ft above high tide line.

27. *Codium saccatum* Okamura, 1915, p. 145, pl. 135, figs. 1–5.

A single specimen of this species was included in a small assortment of algae collected from the wash at Midway Island by Dr. Hubert Frings and sent to me by Dr. Doty. This *Codium* is characterized by its thin, tough, membranous sac-like form and its very small utricles. It has been reported rarely outside of Japan (Dawson, 1957:107).<sup>4</sup> Although Midway Island is not included officially within the State of Hawaii, geographically it is part of the archipelago and hence the basis for including *C. saccatum* in this list.

COLLECTION: *Doty 19699*, in wash, Midway Island, April, 1962, collected by Dr. Hubert Frings.

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<sup>3</sup> See the discussion in Taylor, Joly, and Bernatowicz (1953:103–105).

<sup>4</sup> In personal correspondence Dr. Paul Silva reports that this species has appeared also from Tonga Island, in collection No. 13206 of the Capricorn Expedition.

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# Chromosome Numbers in Some Pacific Pteridophyta

G. BROWNLIE<sup>1</sup>

**ABSTRACT:** Haploid chromosome complements are recorded for two species of Psilotaceae, and for 36 species and one variety of ferns (27 species from New Caledonia, 7 species and 1 variety from New Zealand, and 1 species from New Guinea).

It is suggested that *Schizaea fistulosa* Labill. and *Schizaea fistulosa* var. *australis* Gaud. are specifically distinct. A further suggestion is made that the cytologically varied species of *Lindsaea* together with such genera as *Loxsonia* and *Leptolepia* may constitute a distinct fern family.

THE VALUE OF CYTOLOGICAL RECORDS of the type listed below lies in the contributions they can make to an understanding of relationships within groups of plants. Information such as this complements earlier morphological work, and can be used only in conjunction with such records, for it is in itself merely another morphological criterion. It can either support previously held views or point the way to more detailed research and possible re-examination of certain accepted relationships.

The majority of chromosome numbers listed here are from New Caledonian species of ferns, this island having been selected because of the great interest that its flora arouses in relation to phytogeography and plant relationships in the Pacific. This island possesses in its fern flora species and genera which are less closely allied to recent Malaysian forms than those in the bulk of Pacific island floras. In this respect it is similar to New Zealand.

Reasonable samplings of chromosome numbers in ferns have already been done in Ceylon (Manton & Sledge, 1954), Malaya (Manton, 1954), New Zealand (Brownlie, 1954, 1957, 1958, 1961), and in India by Mehra and his associates (Mehra, 1961). These samplings come from the two extremities of the arc from continental Asia to New Zealand, so that any records from the area between are of particular interest.

## NOTES ON CRITICAL GENERA

### *Schizaea*

Records of chromosome counts in this genus are few (Lovis, 1958; Brownlie, 1961) but these bear out the generally held belief that the present species are relics only of an old flora. The present two counts would indicate that *Schizaea fistulosa* Labill. and *Schizaea australis* Gaud. should be regarded as two distinct species, the latter confined to mountain and southern areas of New Zealand, the former having a much wider range.

### *Lindsaea*

Several species of this genus from Ceylon and Malaya have been recorded by Manton, mostly with a base number of  $n = 50$ , but the impression that it is probably an unnatural assemblage is suggested by the numbers of  $n = c.40$  and  $c.47$  for two species listed here and of  $n = 34$  and  $c.42$  for two other species (*L. linearis* Sw. and *L. trichomanoides* Dry.) from New Zealand. It is possible that here we have two morphologically parallel groups representing two geologically widely-spaced periods of development, those of the  $n = 50$  group being a recently diversified section comparable with such modern families as the Aspleniaceae and the Polypodiaceae, and the other section being remnants of a much older flora. Several species of this older group occur in New Caledonia, but cytological information on these is still lacking. Manton (1958) has already indicated the complexity of Copeland's Pteridaceae.

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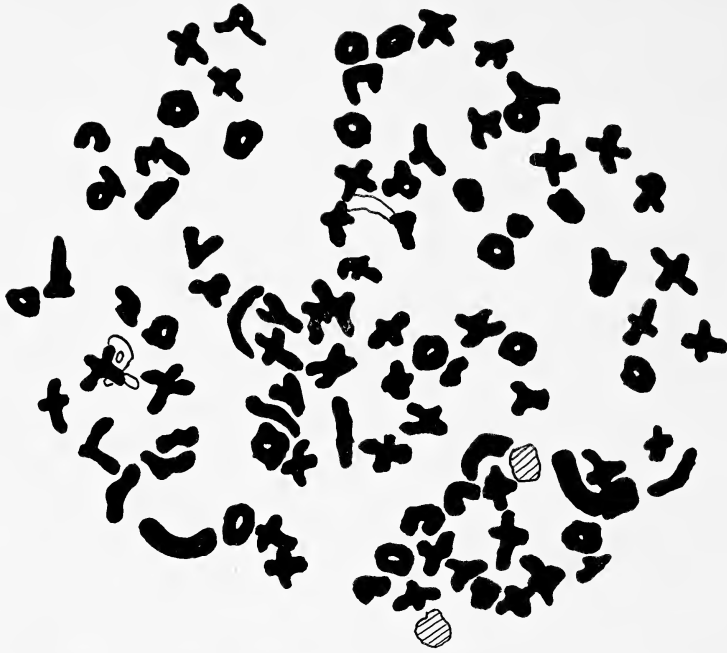


FIG. 1. Meiosis in *Schizaea fistulosa* Labill. var. *australis* Gaud.  $n = 94$ .  $\times 1250$ .

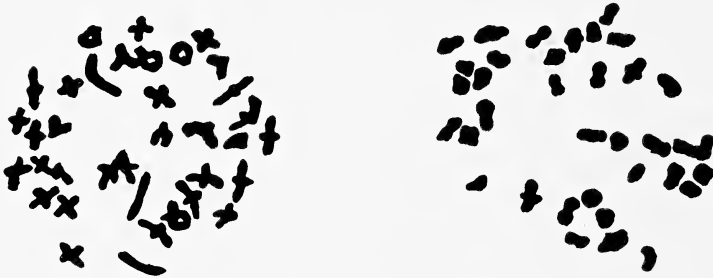


FIG. 2 (left). Meiosis in *Hymenophyllum atrovirens* Col.  $n = 36$ .  $\times 750$ .  
FIG. 3 (right). Meiosis in *Hymenophyllum rufescens* T. Kirk.  $n = 36$ .  $\times 750$ .



FIG. 4 (left). Meiosis in *Lindsaea vieillardii* Mett.  $n = c.47$ .  $\times 1000$ .  
FIG. 5 (right). *Pteris ensiformis* Burm.  $n = 58$ .  $\times 1250$ .

*Loxsonia*

The rather isolated position of this genus has been accepted in most classifications where, in association with the Central American *Loxosomopsis*, it is elevated to the position of a distinct family. Cytologically this genus appears to be related to the older section within *Lindsaea*.

Also to this group probably belongs the genus *Leptolepia*, with a chromosome complement of  $n = c.47$  (Brownlie, 1961).

*Teratophyllum*

This genus was placed in close association with *Bolbitis* and *Elaphoglossum* by Holttum



FIG. 6 (left). Meiosis in *Pteris novae-caledoniae* Hook.  $n = 58$ .  $\times 1250$ .  
FIG. 7 (right). *Tectaria seemanni* (Fourn.) Copel.  $n = 40$ .  $\times 1250$ .



FIG. 8 (left). Meiosis in *Cyclosorus invisus* (Forst.) Copel.  $n = 36$ .  $\times 1250$ .  
FIG. 9 (right). *Blechnum obtusatum* (Labill.) Mett.  $n = 33$ .  $\times 750$ .

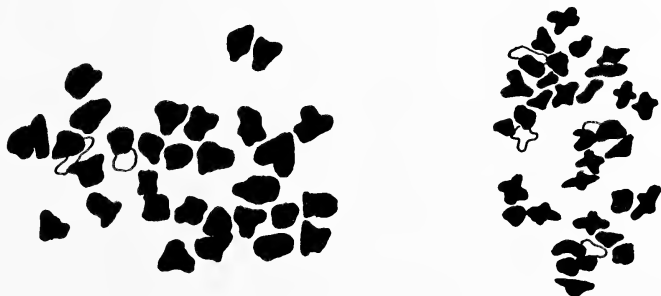


FIG. 10 (left). Meiosis in *Blechnum moorei* C. Chr.  $n = 33$ .  $\times 1250$ .  
FIG. 11 (right). *Drynaria rigidula* Bedd.  $n = 37$ .  $\times 1250$ .

TABLE 1  
LIST OF SPECIES AND CHROMOSOME NUMBERS

SPECIES	LOCALITY	CHROMOSOME NUMBER
<i>Tmesipteris tannensis</i> (Spreng.) Bernh.	Westland, N. Z.	n = c.108
<i>Psilotum nudum</i> (L.) Beauv.	Yaté, New Cal.	n = c.210
<i>Schizaea fistulosa</i> Labill.	Takaka, N. Z.	n = c.270
<i>Schizaea fistulosa</i> var. <i>australis</i> Gaud. (Fig. 1)	Upper Waimakariri, N. Z.	n = 94
<i>Gleichenia dicarpa</i> R. Br.	Plaine des Lacs, New Cal.	n = 22
<i>Gleichenia brackenridgei</i> Fourn.	Mt. Koghi, New Cal.	n = 34
<i>Gleichenia flabellata</i> R. Br.	Col. d'Amieu, New Cal.	n = 34
<i>Hymenophyllum atrovirens</i> Col. (Fig. 2)	Dunedin, N. Z.	n = 36
<i>Hymenophyllum refuscens</i> T. Kirk (Fig. 3)	Otira, N. Z.	n = 36
<i>Hymenophyllum malingii</i> (Hk.) Mett.	Otira, N. Z.	n = 36
<i>Trichomanes dentatum</i> v.d.B.	Mt. Koghi, New Cal.	n = 36
<i>Trichomanes lyallii</i> Hk.	Westland, N. Z.	n = 36
<i>Loxosoma cunninghamii</i> R. Br. ex A. Cunn.	Auckland, N. Z.	n = c.47
<i>Lindsaea vieillardii</i> Mett. (Fig. 4)	Mt. Koghi, New Cal.	n = c.47
<i>Lindsaea prolongata</i> Fourn.	Mt. Koghi, New Cal.	n = c.40
<i>Sphenomeris deltoidea</i> (C. Chr.) Copel.	Chagrin, New Cal.	n = c.88
<i>Pteris ensiformis</i> Burm. (Fig. 5)	Kalabéré, New Cal.	n = 58
<i>Pteris novae-caledoniae</i> Hook. (Fig. 6)	Table Unio, New Cal.	n = 58
<i>Pteris vittata</i> L.	Kalabéré, New Cal.	n = 58
<i>Adiantum hispidulum</i> Sw.	Bouloupari, New Cal.	n = c.175
<i>Adiantum fulvum</i> Raoul	New Plymouth, N. Z.	n = 58
<i>Asplenopsis decipiens</i> Mett.	Mt. Koghi, New Cal.	n = c.58
<i>Davallia solida</i> (Forst.) Sw.	Boguen R., New Cal.	n = 40
<i>Cyathea alata</i> (Fourn.) Copel.	Mt. Koghi, New Cal.	n = 69
<i>Arachniodes aristata</i> (Forst.) Tindale	Col. d'Amieu, New Cal.	n = 82
<i>Bolbitis lonchophora</i> (Kze.) C. Chr.	Col. d'Amieu, New Cal.	n = 82
<i>Teratophyllum wilkesianum</i> (Brack.) Holtt.	Col. d'Amieu, New Cal.	n = c.40
<i>Elaphoglossum vieillardii</i> (Mett.) Moore	Mt. Mou, New Cal.	n = 82
<i>Lastreopsis vieillardii</i> (Mett.) Tindale	Mt. Koghi, New Cal.	n = 41
<i>Lastreopsis tenera</i> (R. Br.) Tindale	Col. des Roussettes, New Cal.	n = 41
<i>Tectaria seemanni</i> (Fourn.) Copel. (Fig. 7)	Col. des Roussettes, New Cal.	n = 40
<i>Cionidium moorei</i> (Hk.) Moore	Hiéngghène, New Cal.	n = 40
<i>Cyclosorus invisus</i> (Forst.) Copel. (Fig. 8)	Bouloupari, New Cal.	n = 36
<i>Diplazium sororium</i> (Mett.) Carr.	Col. des Roussettes, New Cal.	n = c.121
<i>Blechnum obtusatum</i> (Labill.) Mett. (Fig. 9)	Chagrin, New Cal.	n = 33
<i>Blechnum moorei</i> C. Chr. (Fig. 10)	Plateau de Dogny, New Cal.	n = 33
<i>Blechnum indicum</i> Burm.	Golone, New Cal.	n = c.37
<i>Drynaria rigidula</i> Bedd. (Fig. 11)	Mt. Koghi, New Cal.	n = 37
<i>Crypsinus albidosquamatus</i> (Bl.) Copel.	Ilaga Valley, W. New Guinea	n = 36

(1947) in a sub-family Lomariopsidoideae, and by Copeland (1947) close to these same genera in his family Aspidiaceae. Although the present count of  $n = c.40$  is not certain, it supports this association.

#### *Blechnum*

The count of  $n = c.37$  for *Blechnum indicum* appears somewhat unusual because previously this genus appeared to have only two sections, one based on  $n = 28$ , the other on

$n = 33, 34$ . A greater variation in the base numbers gives the impression that the family may be older than has previously been thought.

#### *Other genera*

All remaining figures listed are in accord with previous records for these genera, the only two factors of interest being the constancy displayed by the Hymenophyllaceae in New Zealand, compared with the records from Asia, and the very high polyploidy of the New Caledonian form of *Psilotum nudum*.

## ACKNOWLEDGMENT

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# Pioneer Plants Found One Year After the 1963 Eruption of Agung in Bali

ANWARI DILMY<sup>1</sup>

AGUNG, THE VOLCANO on the Indonesian island of Bali (Fig. 1), erupted in 1843 and caused the death of thousands of people and animals. No complete report has been written about this catastrophe; however, Zollinger (1845) does mention it briefly.

The first indications of the volcano's being active in 1963 were the frequent and recurrent feeble earthquake tremors and shocks felt by some people living in Jehkuri, a village on the southern slope of the volcano at an elevation of 928 m above sea level and at a distance of about 6 km from the summit. The exact times of these earthquake tremors and shocks were not recorded, but they were felt in the afternoon of February 16. The next day weak earthquakes were again felt, this time at Kubu, a seashore village at the northern foot of the volcano. This event caused a slow swinging of hanging lamps.

On the following day, February 18, at about 11 P.M., weak but distinct rumblings were heard for the first time. At 3 A.M. on the 19th some people who were alarmed and had stayed awake all night noticed the first ascent of a thin smoke column which rose vertically upwards. From this moment the activity continued intermittently, with the period of activity lasting for about 1 hr followed by a rest period of 1 hr. On the night of the 19th glows were visible on the northern crater rim.

The periodic volcanic activity continued with increasing intensity until February 20, on which day lava started to flow along the northern slope and nuées ardentes came down along the same direction, causing the death of the first victims at Siligading. The outpouring of lava continued until the middle of March. The length of the stream grew to 7 km and its tongue stopped at an altitude of about 500 m. Day by

day the volcano's activity increased in intensity.

The first paroxysmal eruption started on March 17 at sunrise and lasted for about 7 hr. It was preceded early in the morning two days before by a strong local earthquake. As a consequence of the explosions new breaches appeared in the southern and northern slopes, with the resulting destructive forces reaching a maximum distance of 14 km.

Explosions from the cavity of the crater on March 17 brought an end to the outflow of lava. The characteristics of the andesito-basalt lava, the fact that it began its outpouring in the earliest phase of the eruption, and the fact that its outpouring stopped just before the paroxysmal explosions on March 17, support the theory that this lava was a remainder from the previous eruption of 1843 jammed in the volcano and heated and liquefied in the present eruption.

The number of deaths caused during the first cycle of the 1963 eruption was about 1,100, and about 150 during the second outburst.

Mr. Kusumadinata (1964) of the Geological Survey of Indonesia estimated the volume of the volcanic material energy (Table 1). The total volume of ejected material is about  $280 \times 10^6$  cubic meters. From this estimated volume of ejected material the released thermal and kinetic energy are computed.

Thus the total kinetic and thermal energy, as estimated, amounts to  $8.2 \times 10^{24}$  ergs.

The lava, streams of mud, glowing clouds, nuées ardentes, lapilli, sand and ash killed not only people and animals but also the plants. In May 1963 we made a trip to the Besakih shrine near the resthouse of the Forest Service, on the northern slope of Agung, more than 900 m above sea level. Here we saw nothing but dead plants—trees, shrubs, herbs, and grasses, fungi, ferns, mosses, and lichens. It was very quiet in the neighborhood of the Besakih shrine.

<sup>1</sup> Herbarium Bogoriense of the National Biological Institute, Bogor, Indonesia. Manuscript received June 30, 1964.

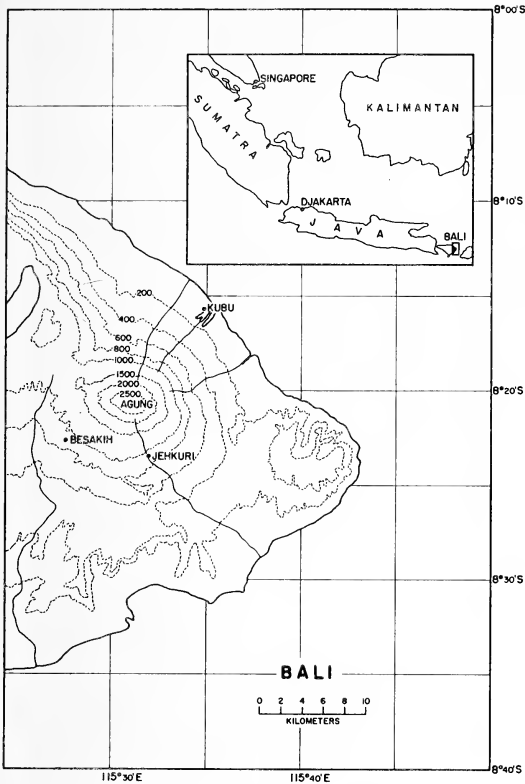


FIG. 1. The part of eastern Bali surrounding the active volcano, Agung, with an inset to show the relationship of this area (in black) to the major islands of western Indonesia.

When the author visited Bali again in October 1963, with Dr. Tarnavski from Rumania and Prof. Jacovlev from Soviet Russia, we still found in the vicinity of Besakih naught but dead plants with the exception of three species which had begun to grow. These exceptions were the Javanese elder, *Sambucus javanica*, the grass *Eleusine indica*, and the herb *Agera-*

*tum conyzoides*. As far as we could see, all other plants were dead.

The third survey during March 1964, was very easy because 90% of the area was still barren. When there were trees at all most of them were dead. Plants were found only near small rivers and on moist sites. With eight helpers we collected the plants and prepared herbarium materials. We could name 75% of the plants in the field; the rest were determined in the herbarium at Bogor.

*Circumstances during the survey of March 1964 and its results*

The circumstances were very different from those in October. Although there was an outpouring of clouds from the volcano every day, no lapilli, sand, or ash were being ejected anymore, so that after the rains started the plants began to grow again. Although the houses were still in ruins and only one or two were occupied, 10% of the ground surrounding the Besakih shrine had a greenish cover of grasses, herbs, shrubs, and trees which had begun to grow, along with several specimens that had sprouted leaves and were growing normally again.

Between the heights of 900 and 1250 m above sea level, 83 species of grasses, herbs, shrubs, and trees were growing (see list below). All the trees planted by the village people, such as *Erythrina*, were still dead, but 90% of the bamboo *Gigantochloa* sp., and of the legume *Leucaena* sp. in the vicinity had begun to grow again. The condition of *Cordia oblique*, which had been propagated by the Agricultural Extension Service years ago, differed from that observed six months previ-

TABLE 1  
MATERIAL AND ENERGY BUDGET FOR THE 1963 ERUPTION OF AGUNG

EJECTED MATERIAL	VOLUME (m <sup>3</sup> )	KINETIC ENERGY (ergs)	THERMAL ENERGY (ergs)
Lava flow	110 × 10 <sup>6</sup>	.....	4.2 × 10 <sup>24</sup>
Nuées ardentes, 1st cycle	50 × 10 <sup>6</sup>	1.6 × 10 <sup>22</sup>	1.9 × 10 <sup>24</sup>
Nuées ardentes, 2nd cycle	20 × 10 <sup>6</sup>	0.67 × 10 <sup>22</sup>	0.7 × 10 <sup>24</sup>
Pyroclastics, 1st cycle	70 × 10 <sup>6</sup>	2.3 × 10 <sup>22</sup>	0.9 × 10 <sup>24</sup>
Pyroclastics, 2nd cycle	30 × 10 <sup>6</sup>	1.01 × 10 <sup>22</sup>	0.4 × 10 <sup>24</sup>

ously: 50% of the trees had begun to bloom again. Of the big trees, several figs and bread-fruit trees were now obviously alive, and 50% of the *Albizzia montana* and *A. procera* had already bloomed.

All the plants mentioned above covered only 10% of the area; the rest of the soil surface was still barren, as if the area had been cemented. No plants of any kind were growing there.

As we reached a height of 1250 m, we found the pine forest of *Pinus merkussii* Yunghuhn and de Vr. all dead and the soil in the vicinity hardened as if cemented. We made three holes in this hardened surface and found the hardening extended to a depth of 10–15 cm. Under this layer we found the needles of the pine trees, which were still undamaged, and directly under this layer of needles the original soil.

There are 316 hectares of pine forest surrounding Besakih, all the trees of which are dead because of the hot clouds, lava, lapilli, or sand and ash from the volcano. This lava mixed with lapilli, sand, and ash formed the cemented upper layer of 10–15 cm.

At an elevation of 1250 m, here and there though still very rare, we discovered nine species of plants: a small *Albizzia montana* tree, a small fig, the bamboo *Gigantochloa apus* Kurz., the grass species *Cynodon dactylon* Pers., *Imperata cylindrica* Beau., *Pennisetum purpureum* Schumacher & Thonn., and *Themeda gigantea* Hack., the herb *Plantago major* Linn., and a small tree of *Sesbania grandiflora* Pers. Of these plants we saw only one or two specimens each. Ninety % of the area was still barren, the surface cemented, and the leafless standing trunks of the pine trees looked like abandoned soldiers. We saw three butterflies but no other living animal.

The following list is of the plants found growing on the northern slope of the volcano, from a height of 900 m above sea level (where the area of the Besakih shrine begins at the resthouse of the Forest Service) up to the 1250 m level, where 90 % of the soil surface one year after the eruption of Agung is still barren. The plants were found along dikes and watercourses.

*Ageratum conyzoides* Linn.  
*Albizzia montana* Benth.  
*Albizzia procera* Benth.  
*Aleurites montana* Wilson  
*Amaranthus spinosus* Linn.  
*Anaphalis viscida* DC.  
*Areca catechu* Linn.  
*Arenga pinnata* Merr.  
*Artocarpus communis* Forst.  
*Artocarpus elastica* Reinw.  
*Averrhoa carambola* Linn.  
*Boehmeria nivea* Gaud.  
*Caesalpinia pulcherrima* Sw.  
*Callicarpa longifolia* Lamk.  
*Centella asiatica* Urb.  
*Centotheca latifolia* Trin.  
*Ceratopteris thalictroides* Brongn.  
*Cheilanthus tenuifolia* Swartz  
*Citrus maxima* Merr.  
*Citrus* sp.  
*Clerodendron serratum* Spreng.  
*Coffea arabica* Linn.  
*Cordia oblique* Willd.  
*Cynodon dactylon* Pers.  
*Cyperus cyperoides* O. K.  
*Cyperus rotundus* Linn.  
*Davallia trichomonoides* Bl.  
*Digitaria sanguinalis* Scop.  
*Drymaria hirsuta* Barttl.  
*Elaeagnus latifolius* Linn.  
*Eleusine indica* Gaertn.  
*Engelhardia spicata* Bl.  
*Equisetum debile* Roxb.  
*Erechtites valerianifolia* Rafin.  
*Erythrina variegata* Linn.  
*Eugenia cumini* Druce  
*Eugenia polyantha* Wight.  
*Euphorbia rothiana* Spreng.  
*Ficus ampelas* Burm.  
*Ficus benjamina* Linn.  
*Ficus septica* Burm.  
*Fimbristylis miliacea* Vah.  
*Flacourtia rukam* Zoll. and Mor.  
*Gigantochloa apus* Kurz.  
*Goniophlebium subauriculatum* DC.  
*Gynoglossum javanicum* Thunb.  
*Hibiscus rosa-sinensis* Linn.  
*Homalomena* sp.  
*Imperata cylindrica* Beauv.  
*Ipomoea batatas* Lamk. (planted)  
*Jatropha curcas* Linn.  
*Kyllinga monocephala* Rottb.  
*Leucaena* sp.  
*Litsea* sp.  
*Lygodium japonicum* Sw.  
*Melia azedarach* Linn.  
*Michelia* sp.  
*Mirabilis jalapa* Linn.  
*Musa* sp.  
*Nephelium* sp.  
*Paederia fortida* Linn.

*Paspalum conjugatum* Berg.  
*Pennisetum purpureum* Schumacher and Thonn.  
*Plantago major* Linn.  
*Pleomele elliptica* N. E. Br.  
*Polygonum chinense* Linn.  
*Pteridium aquilinum* L. var. *Wightianum*  
*Ricinus communis* Linn.  
*Saccharum spontaneum* Linn.  
*Sambucus javanica* Bl.  
*Sesbania grandiflora* Pers.  
*Smilax leucophylla* Bl.  
*Solanum torvum* Sw.  
*Spilanthes nodiflora* Geschn.  
*Terminalia bellirica* Roxb.  
*Themeda gigantea* Hack.  
*Toona sinensis* Roem.  
*Vernonia arborea* Ham.  
*Veronia javanica* Bl.  
*Viburnum lutescens* Bl.  
*Viburnum sambucinum* Bl.  
*Vitex trifolia* var. *heterophylla* Mol.  
*Wedelia montana* Boerl.

Above 1250 m only nine species of plants have been found: *Albizzia montana* Benth., *Cynodon dactylon* Pers., *Ficus* sp., *Gigantochloa apus* Kurz., *Imperata cylindrica* Beauv., *Pennisetum purpureum* Schumacher and Thonn., *Plantago major* Linn., *Sesbania grandiflora* Pers., and *Themeda gigantea* Hack.

At a height of 1400 m the dead pine trees were left standing, while far down in valleys one or two specimens of the following species were observed: *Phragmites karka* Trin., *Sambucus javanica* Reinw., *Pennisetum purpureum* Schum. and Swarz., *Themeda gigantea* Hack., *Engelhardia* sp., *Schima wallichii* var. *noronbae* Bl.

On the slopes of the valleys we discovered: *Polygonum sinensis* Linn., *Cordia oblique* Willd.,

*Dryopteris campestris* Rumph., *Cheilanthes tenuifolia* Swarz., *Coffea* sp., and *Gigantochloa apus* Kurz.

According to these observations upon the pioneer plants in the valleys, the Forest Service should be advised to mix in this forest such pioneer trees as *Engelhardia* sp. and *Schima wallichii* var. *noronbae*, whatever the main species in this forest may be. A monoculture of *Pinus merkussii* is not preferable; experience in Western Europe with monocultures and with the dead forests on the northern and southern slopes of Agung volcano, described above, leads us to believe that a mixed forest, following the example of Nature, is the best reforestation.

It would appear that this devastated area near the 1250 m elevation could be reforested rather readily by digging through the cemented material (to a maximum of 20 cm) and planting seeds or seedlings in the original soil beneath. Though *Casuarina yunghuhniana* Bl. is popular, it does not seem wise to plant it at this high altitude because the needles cover the soil giving other plant species little chance of growing. As a result there would be a good chance, then, that the surface of the soil would suffer serious damage by erosion.

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## Structure and Growth of Mite-induced Galls of *Hoheria sexstylosa* Col.

B. C. ARNOLD<sup>1</sup>

THE FIRST ACCOUNT of mite-induced galls of *Hoheria populnea* A. Cunn was published by Lamb (1952). Attention was devoted chiefly to a description of the gall mite *Eriophyes hoheriae*, and no details of the anatomical structure of the gall were given (Lamb, 1952). Galls of *Hoheria sexstylosa* Col. caused by the same mite were reported eight years later (Lamb, 1960).

The present study is concerned only with *Hoheria sexstylosa*, an evergreen tree widely cultivated in gardens in Christchurch, Canterbury, and often seen to bear galls of varying size and age.

Young galls are greyish-green in colour, shaped like a top, and attached to the smaller branches by a prominent stalk. In older specimens the gall-stalk is generally obscured as the continued growth of the gall encompasses the twig which bears it (Fig. 1). Galls arise also on leaves but this is of less common occurrence.

The salient characteristic of all galls of *Hoheria sexstylosa* is the uneven, creased surface, tufted with grey epidermal hairs, below which the mites live in numerous small cavities.

As the result of insect attacks, dead greyish brown galls are common, but many galls grow vigorously for several years and are readily distinguished by their greener hue from moribund specimens. This perennial habit of proliferation which produces galls up to 4 cm in diameter is often associated with the loss of leaves on the infested branches and a consequent disfigurement of the tree.

Nevertheless trees vary greatly in their propensity to gall formation and it has been observed that two trees may grow close together for several years with branches interlaced, and only one of the trees bears evidence of galls.

The basis of this variation in susceptibility is at the moment unknown.

The chief aims of the present investigation were to find which of the plant organs of *Hoheria sexstylosa* are transformed into galls, to examine the structure of the gall, and to account for the perennial mode of growth.

### METHODS AND MATERIALS

Galls, flower buds, and leaves were fixed at various times throughout the year in formo-acetic-alcohol. Selected specimens from five different trees were embedded in paraffin, and serial sections 10  $\mu$  in thickness were cut and stained in safranin and fast green (Johansen, 1940).

Numerous freehand sections of living galls were also made.

Three unsuccessful attempts were made to induce galls on immature leaves and stem tips of seedlings of *Hoheria sexstylosa*. Twenty-four seedlings about 9 inches high were raised in pots in the glasshouse and used for these experiments.

In winter (July) small slices of living galls containing moving mites and eggs were inserted into three tender, freshly opened leaf buds in each of 10 plants.

A second experiment involved a crude gall extract. Thirty grams of fresh galls were macerated in 200 ml of 30% glycerol (Parr, 1940) in a domestic blender at room temperature. A fluid containing the mites was obtained by expressing the macerated preparation through silk. The fluid was smeared on 30 freshly cut soft stem tips on each of five seedlings. Thirty stem tips of five other plants were smeared with 30% glycerol only.

With the remaining four plants a tap water extract of macerated galls containing moving mites was smeared on freshly cut stem tips in a similar manner except that glycerol was omitted.

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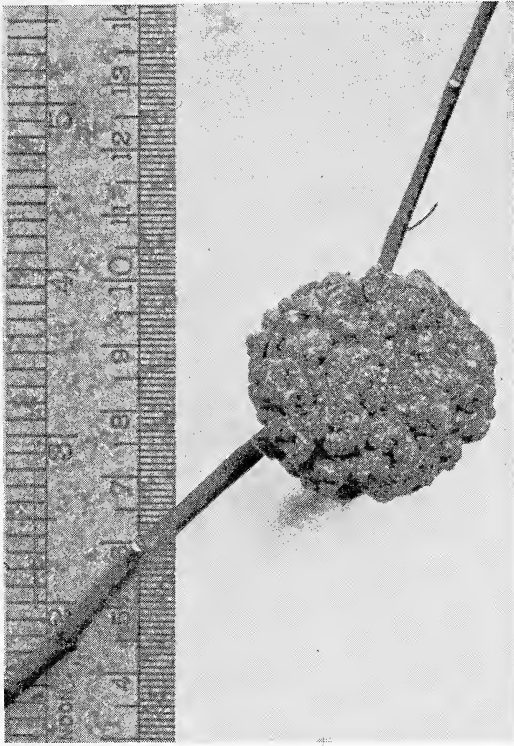


FIG. 1. A large actively growing mite gall.

In all the above experiments plastic bags were kept over the treated plants for a week.

After two years no galls had appeared on any of the plants. It remains to repeat these experiments at other seasons of the year.

#### OBSERVATIONS

The opening of flower buds of *Hoheria sexstylosa* in late summer marks the recrudescence of gall formation. Some infested buds show traces of stunted petals and stamens, but often only the calyx and pedicel remain unchanged, and a mass of convoluted greyish-green tissue takes possession of the interior region. It is the persistence of the pedicel and calyx which gives to young galls their top-shaped appearance (Fig. 2).

A small percentage of unfolding young leaves may develop galls at this time. The distortion may be considerable and the leaf blade may be almost lacking. In other cases leaf development may not be greatly impeded and the galls may be relatively insignificant.

On some trees hardly one in a thousand flower buds escapes attack, so that by autumn the plant is festooned with the new growth of galls and it is difficult to find one seed head on the whole tree.

Sections through living galls show them to consist chiefly of a solid mass of green parenchyma interspersed by clear mucilaginous cells. Within the parenchymatous cells crystals of the druse type are not infrequently encountered. The cavities beneath the surface in which mites can be seen moving are lined by a definite grey meristematic layer. The exterior of the gall is bounded by a well-marked and active periderm.

In older galls the core of the gall is white, being made up of abundant vascular tissues and non-chlorophyllous parenchyma. This massive development of vascular tissues is readily demonstrated by allowing a gall to decompose for a week in tap water. Disintegration of the soft tissues reveals a compact mass of xylem radi-

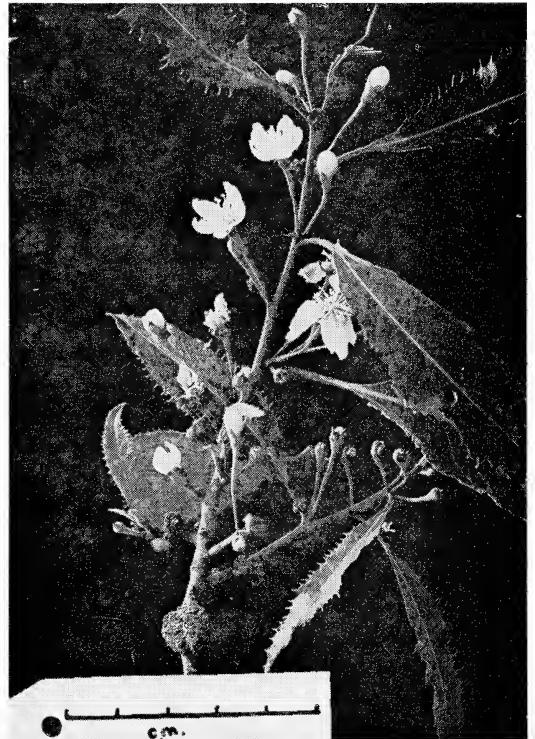


FIG. 2. Flowering twig of *Hoheria sexstylosa* Col., showing some flower buds recently transformed into galls, and one older gall at base.

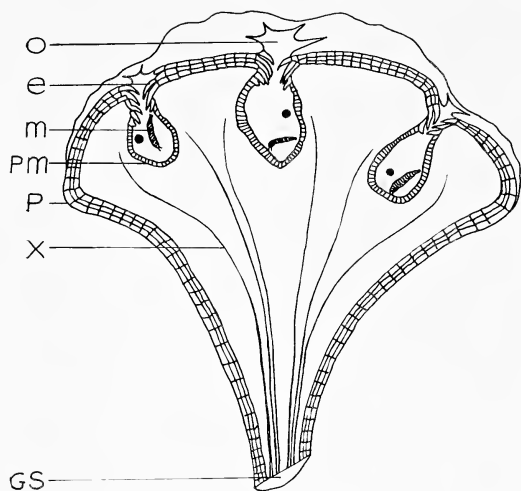


FIG. 3. Diagram of a cut gall (not to scale). *m*, mite; *e*, epidermal hair; *x*, xylem strand; *pm*, pouch meristem; *o*, orifice of mite cavity; *p*, periderm.

ating from the embedded pedicel, and giving the appearance of the spiky "coat" of a chestnut fruit.

The mite-containing cavities are undoubtedly the most remarkable feature of the galls. The mouths of the cavities are irregularly creased (Fig. 3) and surrounded by stout epidermal hairs which are also found in clumps on other regions of the gall surface. The lining of each mite cavity is in fact a sac-like growth centre—a kind of pouch meristem analogous to the shoot growing point of higher plants (Figs. 3 and 4).

Mitotic divisions are found most often within a zone about three cell layers from the cavity. The histological methods used in this investigation were selected to provide a general anatomical picture of the gall and a cytological analysis of mitotic rates was not intended.

What clearly emerges is the fact that perennial growth of the mite-induced galls of *Hoheria sexstylosa* is dependent on the regular activity of the "pouch meristems."

Only at the orifice of the cavities are the epidermal hairs differentiated (Fig. 4), no doubt giving shelter to the colonies of mites below. To the interior of the gall and close to the middle region of the "pouch meristem," xylem elements are seen to differentiate and

lead backwards in an anastomosing system with vascular traces from other mite cavities to unite in the central stalk (Fig. 3). A coherent and efficient conducting system is thus constructed and the gall is able to flourish to the detriment of the rest of the twig (Fig. 5).

To the superficial glance the appearance of *Hoheria sexstylosa* galls, whether borne on leaves or on flower stalks, is of an irregular spherical or conical shape, furrowed by indefinite crevices. But the underlying histogenetic processes of periderm formation, cavity growth, and vascularization are remarkably regular. No essentially different cellular components, except the mites, distinguish the galls from the normal shoot tissues, but the growth pattern is unique.

#### DISCUSSION

So little is known of the biology of *Eriophyes hoheriae* that it is premature to consider in what manner the gall mites may influence growth of galls in *Hoheria sexstylosa*. Whether the mites provide a stimulus in the mechanical act of feeding, or by the liberation of growth substances or enzymes, remains to be investigated.

The preliminary attempts to induce gall formation (described in the section on Methods and Materials) proved ineffective, possibly because the winter season was an unfavourable time. However, other workers have reported promising results from experiments in which galls were artificially induced by extracts from various insects (Bloch, 1954; Boysen-Jensen, 1948; Braun, 1959).

Although the onset of galls in young leaves has been noted at the same time as the galling of flower buds in summer, observation of several trees over a number of years has failed to disclose galling of leaves in spring when there is a mass unfolding of leaf buds. The lack of success in the attempted transmission of mite infection to young leaves in the glasshouse in July, though not very cogent evidence, tends to support the view that new galls arise predominantly in late summer.

The production of galls on leaves would appear to be less favourable to the maintenance of the mite population than the induction of galls on flower buds, which give rise to longer lived galls. Badly galled leaves frequently abscise in

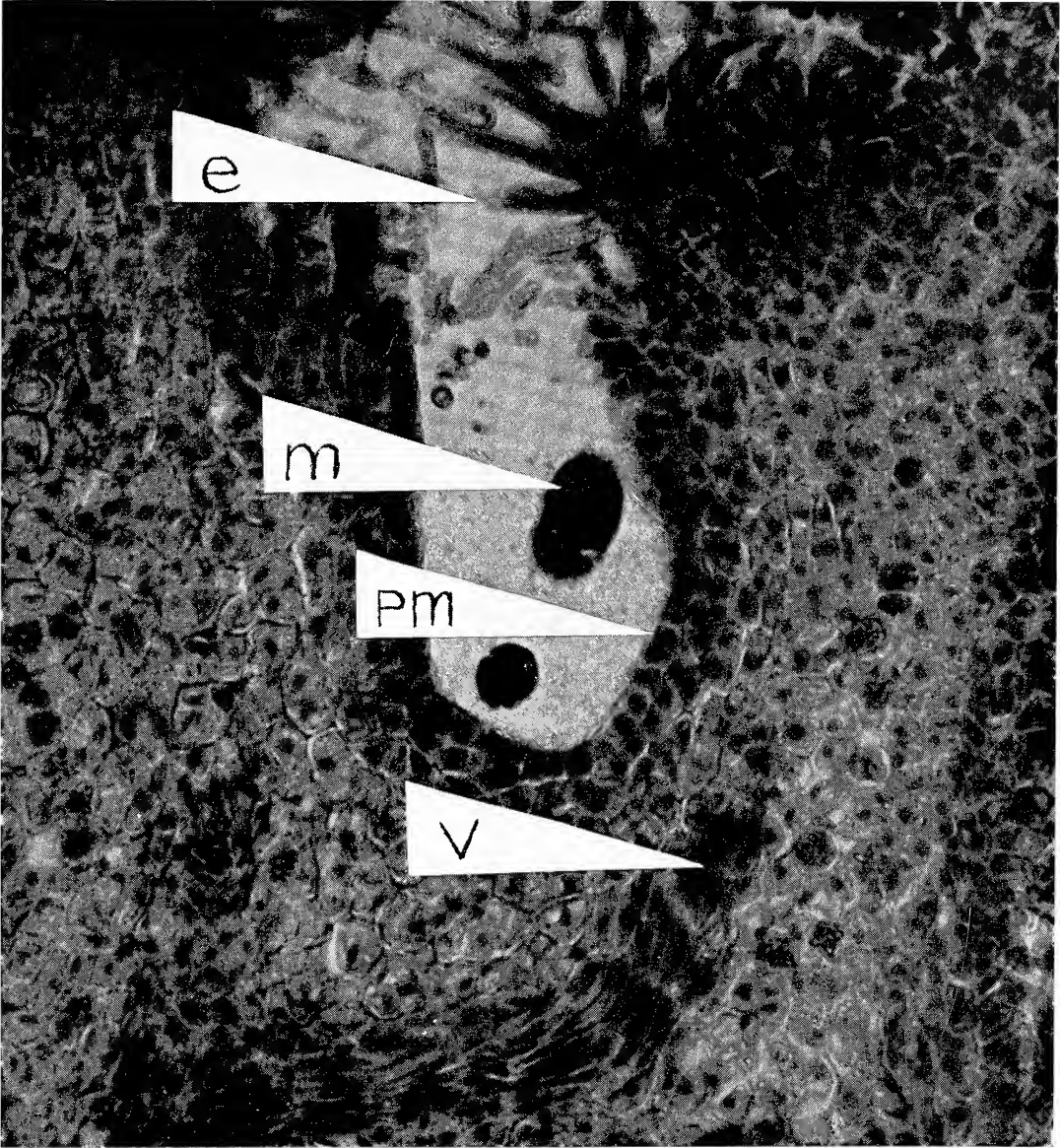


FIG. 4. Longitudinal section through a "pouch meristem,"  $\times 250$ . *m*, section through portion of a mite; *e*, epidermal hair; *v*, vascular strand differentiating; *pm*, inner layer of pouch meristem.

the first three or four weeks, but galls derived from flower buds remain firmly attached by the pedicel, often for several years. It would seem that the tendency to galling of flower buds rather than of leaves represents an evolutionary adaptation favouring the mites.

Furthermore, the mode of enclosure of the mite colonies by the activity of the "pouch meristem" may also be regarded as an evolu-

tionary adaptation shielding the mite colony from the exterior. The majority of eriophyid mites are said to be vagrants on the surface of foliage or in galls of other species of plants (Evans, Sheals, and Macfarlane, 1961).

While one can readily enough draw a parallel between the activity of the "pouch meristem" in *Hoheria* galls and the shoot growing point of angiosperms, it could also be claimed that there



FIG. 5. Defoliation of branch of *Hoberia sexstylosa* Col. caused by galls.

is some analogy with the invaginating growth movements of the developing animal gastrula which is concerned with seclusion and shelter of germinal tissues from the external environment—in the same sense that the embryonic mites are protected from the rigours of the outside world by the invaginated gall-cavity in which they grow.

#### SUMMARY

The solid perennial galls frequently found on cultivated trees of *Hoberia sexstylosa* Col. are caused by the gall mite *Eriophyes hoberiae* Lamb. Most galls arise from transformed flower buds in late summer, but some galls occur on leaves. Persistence of galls often results in leafless unsightly branches.

Within the galls, colonies of mites and their eggs are enclosed in sac-like cavities with puckered mouths, which are ringed by pointed epidermal hairs.

Each cavity is lined by a zone of meristematic

cells which act as a growth region analogous to the shoot growing point of angiosperms.

Vascular traces arise in the vicinity of each "pouch meristem" and differentiate back towards the older vascular strands. In this way is formed an efficient conducting system which radiates from the gall stalk and allows growth of the galls and mites to continue for some years, to the detriment of the rest of the tree.

The cellular make-up of the galls is not essentially different from that of the normal shoot of *Hoberia sexstylosa*, but the pattern of growth is unique and advantageous to the mites and their embryonic young.

#### ACKNOWLEDGMENT

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# The Ternifolia Group of *Macadamia* Species<sup>1</sup>

W. B. STOREY<sup>2</sup>

THE GENUS *Macadamia* (family Proteaceae), as presently understood, comprises ten species of tropical and subtropical evergreen trees (Storey, 1959). One species, *M. hildebrandii* Steenis, is native to Celebes. Three species, *M. rousseii* (Veill.) Sleumer, *M. veillardii* (Brongn. and Gris.) Sleumer, and *M. francii* (Guill.) Sleumer, are native to New Caledonia. The remaining six species, *M. whelani* (F. M. Bail.) F. M. Bail., *M. ternifolia* F. Muell., *M. integrifolia* Maiden and Betche, *M. tetraphylla* L.A.S. Johnson, *M. prealta* (F. Muell.) F. M. Bail., and *M. heyana* (F. M. Bail.) Sleumer, are native to eastern Australia. *M. ternifolia* is the type species upon which von Mueller (1858: 72) established the genus in 1858.

The species of *Macadamia* fall naturally into four distinct intrageneric groups. Group 1: The three extra-tropical Australian species, *M. ternifolia*, *M. integrifolia*, and *M. tetraphylla*. Group 2: The two extra-tropical Australian species, *M. prealta* and *M. heyana*. These species were considered by early botanists to belong to the allied genus *Helicia*. Group 3: The two tropical species of northeastern Queensland and Celebes, *M. whelani* and *M. hildebrandii*, respectively. Group 4: The three tropical New Caledonian species, *M. rousseii*, *M. veillardii*, and *M. francii*. Until they were transferred to *Macadamia* by Sleumer (1955:4-5) in 1955, these species had been placed in the genus *Roupala*.

Regardless of how the members of the three latter groups have been placed generically, there seems to have been no question about their identities as clear-cut, easily recognized species. The identities and typifications of the three species comprising Group 1, however, seem to have become confused almost immediately after

von Mueller established the genus *Macadamia*, with the collection of additional material by various botanists, all of which ended up in herbariums as *M. ternifolia*. The first break in this confusion came with the realization by Johnson (1954:15-18) that the species which, as *M. ternifolia*, as early as 1870 (Anonymous, 1870:1811) had been brought into cultivation in Australia for its edible nuts, was not von Mueller's *M. ternifolia* at all but, instead, was a species which had never been properly described botanically. Consequently, Johnson described it as a new species, *M. tetraphylla*.

The second break came in 1956 when Smith (1956:39-40) recognized that the species which Maiden and Betche (1897:624) described as a new species, *M. integrifolia*, but which later they revised (Maiden and Betche, 1899:150) to *M. ternifolia* var. *integrifolia*, was indeed a valid species in its own right. At the same time, Smith clearly typified *M. ternifolia*. In so doing he pointed out that the species described as *M. minor* and *M. lowii* by F. M. Bailey (1910:11; 1911:127) are only variant forms of *M. ternifolia*, and that the names, therefore, must lapse into synonymy.

In view of the confusion which existed in the past, and which continues to some extent today, especially in horticultural literature, I shall summarize and compare here the salient features of the three species in question, with the hope that this will clarify the delineations which separate the taxons of this so-called *ternifolia* group.

## TYPIIFICATION

The principal taxonomic characters of the three species under discussion are listed in Table 1. Additional notes are given below.

### *M. ternifolia*

VERNACULAR NAMES: Gympie nut; Maroochy nut; small-fruited Queensland nut.

<sup>1</sup> Paper No. 1623, University of California, Citrus Research Center and Agricultural Experiment Station, Riverside, California. Manuscript received April 7, 1964.

<sup>2</sup> Department of Horticultural Science.

INDIGENOUS RANGE: Tropical rainforests of Australia on the eastern slope of the Great Dividing Range, extending from the Pine River northwest of Brisbane in the Moreton Bay District of Queensland northward to Kin Kin in the Gympie District, a distance of about 130 miles; latitudinal range, about  $27^{\circ}30'$ – $26^{\circ}$  S. I saw trees in their native habitat in the Blackall Range near Maleny and in the vicinity of the near-coastal village of Eumundi.

Trees of this species are small in comparison with the other two, seldom attaining heights and spreads exceeding 15 ft. They have a tendency to develop multiple trunks. As noted by Smith (1956:39) "the species is quite distinctive in the field with its smaller leaves, which are reddish on the young shoots, more slender and dark branchlets, pinkish flowers and smaller fruits." The flowers are borne in short sub-terminal axillary racemes on mature terminal

TABLE 1  
PRINCIPAL TAXONOMIC CHARACTERS OF *M. ternifolia*, *M. integrifolia*,  
and *M. tetraphylla*

CHARACTER	<i>M. ternifolia</i>	<i>M. integrifolia</i>	<i>M. tetraphylla</i>
Phyllotaxy	basically, 3 leaves in a nodal whorl; young seedlings may have only 2; occasional branches have 3 or 5	basically, 3 leaves in a nodal whorl; young seedlings usually have only 2; occasional branches have 4	basically, 4 leaves in a nodal whorl; young seedlings usually have only 2; occasional branches have 3 or 5
Leaf attachment	petiolate	petiolate	sessile or scarcely subsessile
Adult leaf shape	lanceolate	oblanceolate to obovate	oblanceolate
Adult leaf margin	scarcely serrate, with 8–10 teeth on side	generally entire; sometimes with 1–12 teeth on a side	numerous serrations, ranging from 15–40 on a side; occasional leaves have fewer than 15
Color of new growth	pink to red	pale green; occasional individuals with bronze tinging	pink to red; occasional individuals yellowish-green, due to lack of anthocyanin
Flower color	pink	white	pink; white or cream colored in individuals lacking anthocyanin
Racemes	2–5 inches long, with 50–100 flowers	4–12 inches long, with 100–300 flowers	6–18 inches long, with 100–300 flowers
Pericarp	grayish-green in appearance due to dense white pubescence; dehisces fully on tree before fruit drops	bright clear green, due to nearly glabrous condition; often fails to dehisce when fruit is still on tree	grayish-green in appearance, due to fairly dense white pubescence; dehisces fully on tree before fruit drops
Seed size	transverse diameter $\frac{3}{8}$ – $\frac{1}{4}$ inch	transverse diameter $\frac{1}{2}$ – $1\frac{1}{4}$ inches	transverse diameter $\frac{1}{2}$ – $1\frac{1}{2}$ inches
Seed shape	commonly fusiform to nearly spherical	commonly spherical	commonly fusiform, some nearly spherical
Seed surface	smooth to scarcely pebbled	generally smooth; rarely with slight pebbling	generally pebbled; infrequently smooth or nearly so
Kernel	bitter; unpalatable	sweet; highly palatable	sweet; highly palatable

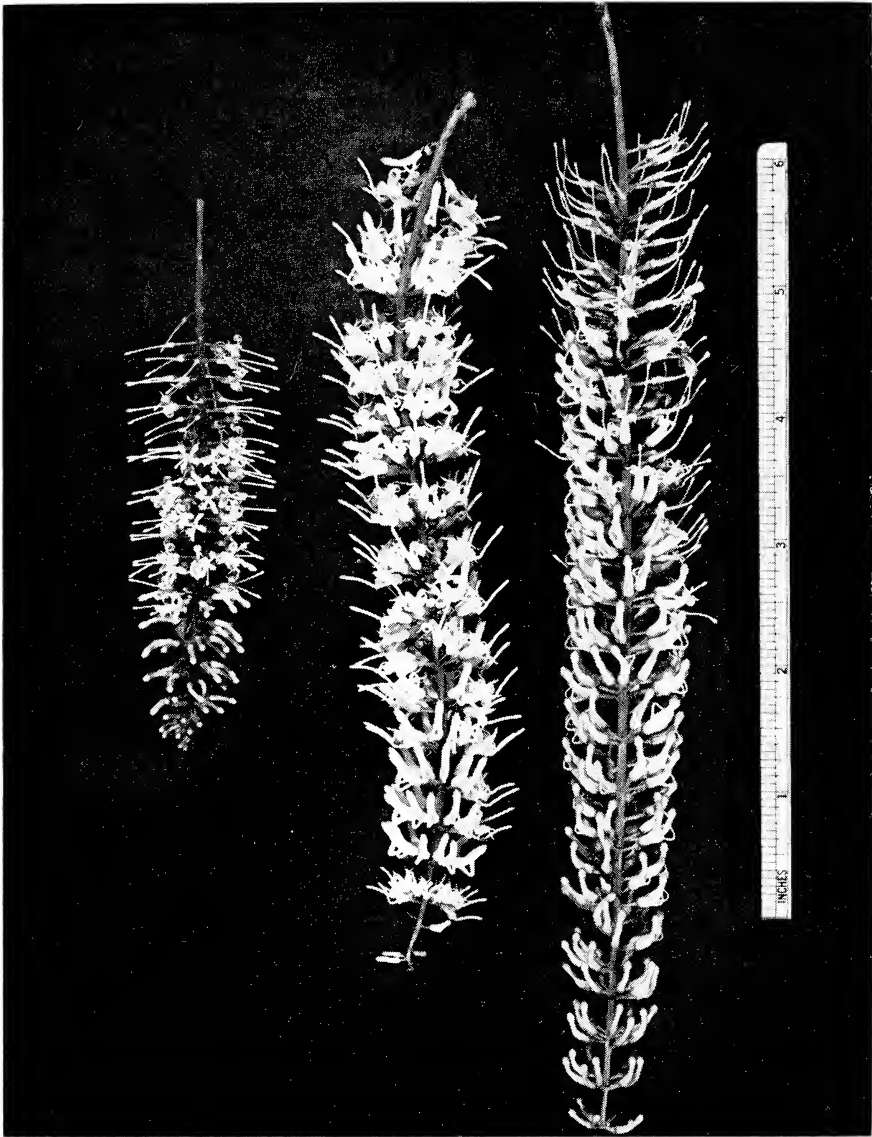


FIG. 1. Racemes of *Macadamia* species. Left, *M. ternifolia*; center, *M. integrifolia*; right, *M. tetraphylla*.

branchlets. The racemes rarely exceed 5 inches in length, with an upper limit of about 100 flowers (Fig. 1). The follicular fruits mature and drop in April in Australia, in November in California. The species is not ordinarily cultivated because the nuts are so bitter that they are unpalatable. They are small in comparison with those of the other species (Fig. 2). The leaves are small, rarely exceeding 6 inches in length and 1 inch in width. The transition which occurs in leaf form from seedlings of

newly initiated branch shoots to the adult, fruiting branch is shown in Figure 3A. The leaves occur in nodal whorls of three to five, but young seedlings may have them initially only in opposite pairs.

Much of the misidentification and confusion among the species resulted from the mixing of transitional forms in the herbarium. A more detailed discussion of leaf forms and variations in nodal numbers has been published elsewhere (Storey, 1963).



It seems unlikely that this species occurred anywhere outside of Australia until the writer introduced it into California in 1960. Pope (1929:3) thought that certain trees on the island of Hawaii belonged to this species, and, because of the bitterness of their nuts, urged their destruction to prevent them from hybridizing with the other two species. I was closely associated with Pope at the time, and was familiar with the trees in question. Having seen both *M. ternifolia* and *M. integrifolia* in their native habitats and under cultivation, I am reasonably certain that the trees in question were not the first species but were a form of the latter in which some bitterness had developed. Bitterness is known to occur in some seedling lines of the species.

*M. integrifolia*.

VERNACULAR NAMES: Macadamia nut; smooth-shell macadamia nut; Queensland nut;

Australian nut; bush nut; nut oak; Bauple nut (sometimes spelled as pronounced, Bopple, or corrupted to Popple).

INDIGENOUS RANGE: Coastal and tropical rainforests on the eastern slopes of the Great Dividing Range in Queensland, extending northward from the Numinbah Valley, which lies immediately to the north of the McPherson Range of mountains that forms the boundary between Queensland and New South Wales, to the lower Mary River near Maryborough, a distance of about 275 miles; latitudinal range, about 28°–25° S.

The trees of this species are large and spreading, some attaining heights of 60 ft or more and spreads of 50 ft. The branchlets are lighter colored than those of *M. ternifolia*. New flushes of growth generally lack any reddish or pinkish coloration. Juvenile leaves are long, linear-lanceolate, the adult leaves usually becoming entire or nearly so (Fig. 3B). Adult leaves measure 4–12



FIG. 2. Seeds of *Macadamia* species. Top, *M. ternifolia*; left, *M. integrifolia*; right, *M. tetraphylla*.

inches in length and 1–3 inches in width. They occur in whorls of three or four, with three by far the most common. Young seedlings and new shoots may have them in opposite pairs. The inflorescences are borne on mature branchlets, usually on the growth increments produced in the top two or three, or more, seasons preceding the most recently matured ones. The flowers are white. The racemes upon which they are borne vary among individuals, from as short as 4 inches to as long as 12 inches or more. The number of flowers on the racemes ranges from 100 to 300 (Fig. 1). The bulk of the crop matures from March to June in Australia, July to November in Hawaii, and November to March in California. However, some fruit is produced almost every month in the year, consequently the species is sometimes called "everbearing."

Although this species was not recognized as new and given a specific epithet until 1897 (Maiden and Betche, 1897:624), it was introduced into California as a potential economic plant, under the invalid name *M. ternata*, in 1879 by the University of California College of Agriculture (1881:66) and planted on the campus at Berkeley in 1882 (Butterfield 1963:48). Two trees of this introduction continue to grow on the Berkeley campus. Almost simultaneously, at a time reported to be between 1881 and 1885 (Pope 1929:2; Thevenin 1961:15), W. H. Purvis of Honokaa, Hawaii, introduced the species, as *M. ternifolia*, which he planted at Kapulena. A second introduction into Hawaii was made in 1892 by E. W. and R. A. Jordan who planted the trees at the former's home on Wyllie Street in Honolulu (Pope 1929:2). This introduction became the source of the principal commercial varieties cultivated in Hawaii today.

#### *M. tetraphylla*

VERNACULAR NAMES: Macadamia nut; rough-shell macadamia; spiny leaf macadamia; rough-shell Queensland nut; Australian nut; bush nut.

INDIGENOUS RANGE: Tropical rainforests on the eastern slopes of the Great Dividing Range, extending from the Richmond River near Casino and Lismore in northeastern New South Wales to the Coomera River in the vicinity

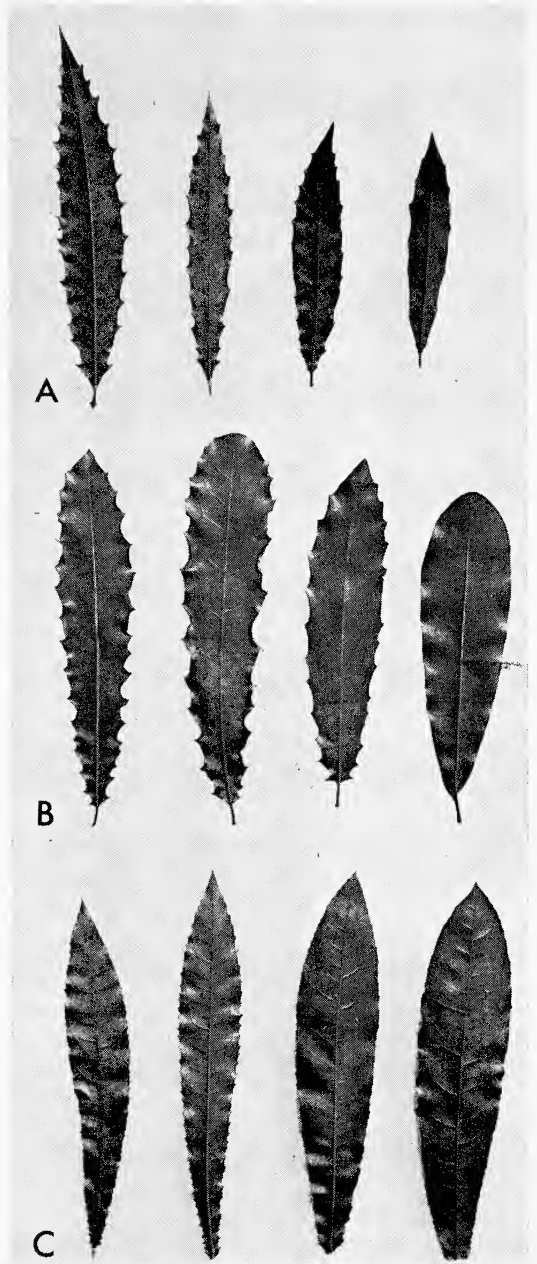


FIG. 3. Leaf transitions in *Macadamia* species, from juvenile on the left to adult on the right. A, *M. ternifolia*; B, *M. integrifolia*; C, *M. tetraphylla*.

of Beechmont and the Nerang River in the vicinity of Advancetown in the southeastern corner of Queensland, a distance of about 75 miles; latitudinal range, about 29°–28° S.

The trees of this species are large and spread-

ing, sometimes attaining a height of 50 feet and a spread of 60 feet. The branchlets are usually dark colored, although not quite so dark as those of *M. ternifolia*. The young leaves on new growth are generally flushed with red or pink coloration. Occasional trees may be seen, however, which lack anthocyanin pigmentation and, consequently, have new leaves which are pale yellowish green in color. Juvenile leaves are long, linear-lanceolate. Adult leaves differ little from juvenile leaves except in being somewhat broader (Fig. 3C). Adult leaves measure 4–20 inches in length and 1–3 in width. They occur most commonly in whorls of four, although an occasional branch may have three or five; and, in young seedlings, they generally occur in opposite pairs. The racemes are borne in the proximal axils of the most recently matured two or three increments of growth. The racemes vary from 6–18 inches in length, and the number of flowers from 100 to 300 (Fig. 1). In the vast majority of trees the flowers are bright pink. In the occasional individuals which lack anthocyanin, however, they are white or cream colored. The crop matures from March to June in Australia, from March to June in Hawaii, and from September to January in California. There is no tendency toward ever-bearing in this species, consequently the entire crop is seasonal.

This species, as noted previously, was not recognized as new and different from *M. ternifolia* until 1954, when it was so recognized by Johnson (1954:15). By this time it had been in cultivation, as *M. ternifolia*, for 84 years. There is little doubt that it is the one referred to by an anonymous writer in 1870. Its introduction into commercial orcharding occurred about 1890, with the planting of about 250 trees on the K. C. Fredrickson property at Rous Mill, N.S.W. I visited this orchard, which is still in production, in 1960. The species was introduced into Hawaii by the Board of Agriculture and Forestry of the Government of Hawaii in 1892–94 for use in reforesting the slopes of Mt. Tantalus back of the city of Honolulu (Pope 1929:2). There seems to be no record of when and by whom it was introduced into California. The oldest trees I have

seen appear to be 50–60 years old. They occur only in San Diego, Orange, and Los Angeles counties in southern California.

#### CYTOLOGY AND GENETICS

All three species have the identical somatic chromosome number of  $2n=28$ . Insofar as I know, this report is the first on the chromosome numbers of *M. ternifolia* and *M. tetraphylla*. I determined these numbers from root tips of *M. ternifolia* and *M. tetraphylla* seedlings, and from dividing microsporocytes in *M. tetraphylla*.

The chromosome number of *M. integrifolia* was first reported (Darlington and Wylie, 1955:90) as " $2n=28$  (56)," as a previously unpublished number determined by Ukio Urata of the University of Hawaii. The 56 in parentheses refers to a clone, Y-279, which was discovered to be tetraploid. Later, Urata (1954:12) published the numbers as " $n=14$  and  $n=28$ ," under an old, lapsed synonymous name, *M. ternifolia* F.v.M. var. *integrifolia* (Maiden and Betche) Maiden and Betche. I am familiar with Urata's material, since I served on the committee for his Master of Science thesis which served as the basis for the publication cited. The chromosome number reported for this species is confirmed in a recent paper by Ramsay (1963:9).

Johnson (1954:18), Beaumont (1956:17), and Smith (1956:40), have pointed out that a number of trees occurring in the Numinbah Valley and in tributary valleys of the Coomera River in southernmost Queensland have characters which strongly suggest that they are hybrids between *M. integrifolia* and *M. tetraphylla*. The region in question is the one in which the ranges of the two species come together and overlap to some degree. Beaumont collected cuttings of several specimens in 1953, which he sent to Hawaii and California to be propagated. These have flowered and fruited in recent years and, from close observations on them, there seems to be every reason to believe that they are indeed hybrids. Meanwhile, similar trees have been found in Hawaii and California among seedlings produced from seeds collected in orchards where the two species

grow together (Hamilton and Fukunaga, 1959: 7). Despite their putative interspecific hybrid origin, such trees are highly fertile.

Although the natural range of *M. ternifolia* lies completely within that of *M. integrifolia*, the two species are not found growing together. Nothing which might be construed to be a natural hybrid between them has been reported. I know of no attempt which has been made up to the present to hybridize *M. ternifolia* with either *M. integrifolia* or *M. tetraphylla*. Consequently its cross fertility with those species and the fertility of any hybrids which might be produced is unknown.

#### GRAFT COMPATIBILITY

Recent experiments in grafting have shown that the three species are mutually graft-compatible in any combination, whether used as rootstocks or scions (Storey and Frolich, 1964: 54–58). The degree of compatibility is so high that there is no observed tendency of any one species to overgrow the other at the graft union.

All attempts to graft *M. integrifolia* and *M. tetraphylla* on *M. prealta* and *M. whelani* have failed. Attempts to graft those species on *Grevillea robusta* A. Cunn. and *G. banksii* R. Br., closely related species in the family *Proteaceae*, also have failed.

#### SUMMARY AND CONCLUSIONS

This paper enumerates the ten species which comprise the genus *Macadamia* as it is presently understood. These fall into four clear-cut intrageneric groups. Species identification and typification in three of the groups have given no difficulty to systematic botanists and horticulturists in the past. The fourth group, however, which consists of the three species *M. ternifolia*, *M. integrifolia*, and *M. tetraphylla* and is commonly referred to as the "ternifolia group," was a source of confusion taxonomically for almost a hundred years.

Much of the confusion among the species undoubtedly resulted from the fact that everything that was collected in the field in the early years was placed under *M. ternifolia* in the

herbarium. It is understandable how botanists working on such material in the herbarium came to regard *Macadamia* as a single highly polymorphic species, especially when one considers the overlapping ranges, the similarity of juvenile shoots and leaves, the transitional forms of leaves between the juvenile and the adult, and other factors, added to which is the possibility that the collections included some interspecific hybrid material. It is noteworthy, however, that most of the confusion and uncertainty one experiences from the study of pressed herbarium specimens is dispelled when he sees the trees in the field, for the species are so different in size and aspect that there is little doubt about their being distinct taxons.

That the three species are indeed closely related in a group set apart from the other species of *Macadamia* is attested by their high degree of mutual graft compatibility, by identical chromosome numbers, by the genetic cross-compatibility between two of the species, and by the high order of fertility of the interspecific hybrid. One can speculate that they arose from a single ancestral intrageneric prototype, and that the characters which distinguish one from another represent accumulations of gene changes over a long period of time which have not, however, affected chromosome homology. The occurrence of fertile hybrids is of interest, because it opens the way to genetic studies and to the possible improvement of horticultural varieties in a plant breeding program.

Superficially, the natural habitats of the species appear to be identical, and their natural requirements with respect to rainfall and soil factors to be the same. *M. integrifolia* and *M. tetraphylla* are often grown side by side in orchards in Australia, Hawaii, California, and elsewhere. In Australia cultivated trees of the former are to be seen as far south as Sydney. Trees of the latter are to be seen as far north in Queensland as Rockhampton. A matter for conjecture, therefore, is why the natural range of each is restricted to a comparatively small region, and why the ranges end so abruptly where they come together immediately north of the McPherson Range. This should make an interesting study in plant ecology.

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# On Populations in Antarctic Meltwater Pools

CHARLES W. THOMAS<sup>1</sup>

**ABSTRACT:** In meltwater pools of the Clark Peninsula area of Antarctica fresh water biota spend most of the year frozen into the ice or in underlying sediments.

In the absence of dynamic pressure (as is the case in pools), ice exerts no pressure on organisms.

Survival of organisms appears to be a function of their ability to dehydrate or encyst.

*Brachionus* and cosmopolitan forms have been introduced into Antarctica. The most likely agency of transport is skua gulls.

WATER SAMPLES taken from 12 meltwater pools on the Knox Coast, Wilkes Land, Antarctica show that the majority of them support myriads of animalcules. This is remarkable because these organisms spend most of the year frozen into solid ice or bottom sediments and in the absence of light. We will discuss here reasons for survival, freedom from ice-crushing, and means by which biota may have been introduced into Antarctica.

The collection of specimens and data for this study was made on Clark Peninsula and on an unnamed islet one mile northeast thereof, (66°18'S). This area on the Knox Coast of Wilkes Land has been described in some detail by Hollin and Cameron (1961). Collecting was done during the construction of a permanent scientific base on Clark Peninsula, January 27 to February 11, 1957.

Clark Peninsula, which is generally ice-free, is a headland about 5 km long and with a maximum width of 4 km. A snow field covers approximately 30% of the land area. The south end of the peninsula is overridden by inland ice which terminates in a moraine. At the time of pool sampling, ablation of the snow field had begun.

Twelve pools were sampled at the height of the antarctic summer. These had probably been

ice-free less than two weeks.<sup>2</sup> Since freezing began in late February the pools, in 1957, were ice-free less than two months. Hollin and Cameron (supra cit.) indicate that the summer of 1957 was milder than average and that hardly any melting was apparent in February, 1959.

Descriptive information concerning the pools is shown in Table 1.

## METHOD OF STUDY

Samples were collected from the pools by immersing quart jars near the bottom and allowing them to fill. Specimens for microscopic examination were meted into a watch glass or onto slides. After about 1 cc of sampled water from each pool was examined, the water was filtered through a plankton well and the concentrate preserved in 70% alcohol for further study and more positive identification of organisms. The water was then tested for salinity with a Digby and Bigg Ionic meter.

Organisms which could be identified are listed in Table 2. It is difficult to establish a criterion by which abundance of organisms may be indicated in such a heterogeneous population. A common numerical abundance of large forms might mean a paucity of small ones. Hence, the terms "abundant," "common," "few," and "rare" are relative rather than absolute.

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<sup>2</sup> Temperatures may be generally above freezing in January, but the insulating effect of snow-cover and sublimation delays thawing until ablation occurs.

The inventory in Table 2 is not complete. Many specimens were damaged beyond identification by violent churning during the rough voyage from Antarctica to Australia. This damage was probably aggravated by inadequate preservation.

#### DISCUSSION

While no observations were made of ice thickness in the pools considered here, John T. Hollin (personal correspondence) says the ice must have been at least 30 cm thick in the autumn and 100 cm thick in the winter, and that vehicles were freely driven across the pools. The present author, moreover, observed a pool approximately 30 cm deep frozen solid on March 5, 1956 at Ross Island (78°S). According to List (1951), about 0.98 lys. min<sup>-1</sup> of

solar radiation would have reached that position at the time. The same amount of energy is available to Clark Peninsula on April 1. Hollin (op. cit.) reports the pools are wind-swept with about 3 cm of fresh snow overlying several centimeters of sublimation. While the latter is quite significant, the snow-cover alone completely insulates the ice<sup>3</sup> and all organisms must have been frozen either into the ice or in underlying sediments before mid-April.

Hollin (op. cit.) accounts for salinity in the pools by heavy Quaternary glaciation of Clark Peninsula. After retreat of the ice the land was uplifted 30 m and, since the pools lie at a lower elevation, they were formerly pools of sea water.

<sup>3</sup> The albedo being ca. 72% only about .0081 lys. min<sup>-1</sup> could penetrate 3 cm of fresh snow (Thomas, 1963).

TABLE 1

LOCATION AND DESCRIPTION OF POOLS FROM WHICH SAMPLES WERE TAKEN IN THE CLARK PENINSULA AREA OF WILKES LAND, ANTARCTICA, JANUARY AND FEBRUARY, 1957

POOL NO.	LOCATION	ELEVATION (ABOVE MLW) m	APPROX. AREA m <sup>2</sup>	APPROX. DEPTH cm	SALINITY ‰
1	Wilkes Station, near meteorology building	7	140	30	1.6
2	Wilkes Station, water supply	14	340	45	0.8
3	North central side of Clark Peninsula	3	170	40	6.6
4	Northeast central side of unnamed islet	3	900	40	3.5
5	Northeast central shore of Clark Peninsula, in a creek	2.5	10	25	10.2
6	Northeast central shore of Clark Peninsula, mouth of a creek	1.5	1,000	100	24.3
7	Wilkes Station, rocky ledge above meteorology building	9	19	35	5.0
8	Clark Peninsula, 2 km southeast of station, in a creek	4	280	30	4.8
9	Pot-hole on northeast side of Clark Peninsula, near penguin rookery	12	12	30	0.6
10	Northeast side of Clark Peninsula, in a penguin rookery	3	9	20	11.2
11	Pot-hole on northeast side of Clark Peninsula, in a penguin rookery	10	4	35	0.9
12	East corner of Clark Peninsula, near lagoon	3	12	25	14.8



He believes there is a marked stratification of salinity due to meltwater in the upper layers. The present author observed that nearly all pools are subject to contamination in some degree by spray when sea ice is absent. Pool 6 (S ‰ 24.3) is periodically invaded by sea water. Pools 2, 9, and 11 are continually flushed during ablation of the snow field. The presence of fresh water forms in pool 6 may be accounted for by stratification, in which meltwater occupies the upper layers, and by migration of biota from a higher pool.

That lower forms of life can be frozen into ice and revived upon thawing has been observed by several authors. Kapterev (1936) found that *Cyclops* and *Planorbis* survive after being thawed out of shallow pools near the Amur River. He observed 20 genera of extant algae and a crustacean revived after being thawed from permafrost, in which he estimates they might have been frozen a thousand years. Luyet and Gehenio (1940) include tardigrades, rotifers, paramecia, euglenids, amoebae, and diatoms with organisms which survive extreme cold.

The present author obtained, simultaneously, three samples from a pool in Massachusetts, the surface of which was frozen. One sample was not frozen. A second was frozen solid under natural conditions for a week. The third was frozen into solid ice in less than two hours and maintained at  $-15^{\circ}\text{C}$  in total darkness for a month. When the two frozen samples were thawed no mortality was apparent. The following organisms were found in the three samples: *Rhizoclonium cladophora*, *Melosira varians*, *Fragilaria* sp., *Tabellaria* sp., *Navicula* sp. A and B, *Rophaloidia* sp., *Amphora* sp., *Epithemia* sp., *Chilamonas paramecium*, *Urostyla* sp., *Tintinnopsis* sp., *Paramecium* sp., *Chaetogaster* sp., Bdelloid rotifers (four genera).

According to Scholander et al. (1955) a great many aquatic plants and animals (including *Daphnia*) spend the winter frozen into the ice of lakes and pools in the Arctic. Similar observations have been made by others.

Luyet and Gehenio (supra cit.) examined causes of death of organisms due to freezing as postulated by several authors. They conclude, "How enormous hydrostatic pressures have no

action on protoplasm while pricking on a glass needle may, in some instances, start coagulation is entirely unknown." In the nineteenth century, bursting of cells by ice formation was widely believed to cause death.

According to Plateau (1872), "... it is a known physical principle that the cavities in a solid body expand like the body itself. Therefore, the cell contents cannot be crushed by freezing." He illustrated this observation with an apparatus consisting of a glass tube on the end of which was a rubber bulb filled with a liquid, and immersed vertically, the open end up, in a flask containing water. When the latter froze in the flask, the level of the fluid in the tube remained unchanged. This indicated that no pressure was exerted on the rubber bulb. Luyet and Gehenio take issue with Plateau on the grounds that (according to them) the results of his experiment disagreed with the principle he sought to invoke. "He should have observed a lowering of the level of the fluid in the manometric tube if the cavity around the tube were expanding."

But Plateau was right. Ice seamen are familiar with this principle. A thin-skinned ship may be frozen into static ice without damage (Dieck, 1885). For several years, the gasoline tankers (YOGs) were frozen annually into the ice in Arrival Bay, Antarctica. While the cavity created by the ship expands, new ice forms at the same rate between the ice-body and the vessel's hull. Hence, an animal frozen into ice becomes an integral part of the system without being subject to pressure.

The experiments of Scholander et al. (supra cit.) and of Kanwisher (1955) show that resistance to cellular freezing runs parallel with the ability of an organism to withstand dehydration. From the observations of Becquerel (1936) it appears that, in general, the lower forms enjoy this ability to a greater extent than do the higher ones.

The rotifers and some other animals in Table 2 were identified by Dr. C. R. Russell of Canterbury University, Christchurch, New Zealand. He says (personal correspondence) the rotifers *Brachionus quadridentatus* and *B. calyciflorus* are generally found in temperate waters and the lowest temperature in which these species



TABLE 2  
POPULATIONS OF MELTWATER POOLS ON CLARK PENINSULA AND AN UNNAMED ISLET, ANTARCTICA

ORGANISMS	POOL NUMBER											
	1	2	3	4	5	6	7	8	9	10	11	12
FLORA												
CHLOROPHYCEAE												
<i>Pleurococcus antarcticus</i> W. and G.S. West					C*	C	A					C
<i>Pleurococcus</i> sp.			A		A	A	C	C		A		C
<i>Prasiola</i> sp.										C		
<i>Chlamydomonas intermediata</i> Chodat.			F	F	A					A		A
<i>Chlamydomonas</i> sp. A	A				A							C
<i>Chlamydomonas</i> sp. B					C							A
<i>Pandorina</i> sp.												C
CHRYSOPHYCEAE												
<i>Cocconeis wiekenis</i> Petit							C					A
<i>Cocconeis</i> sp.					A		C	A		A		
<i>Cyclotella operculata</i> Kutzing				R								
<i>Melosira</i> sp.					C		F					
<i>Corethron</i> sp.						R						
<i>Fragillaria curta</i> Van Heurck						R						
<i>Navicula borealis</i> (Ehrenberg)					A	A						A
<i>Navicula murrayi</i> W. and G.S. West			F	R	A	A	C					
<i>Navicula shackeltoni</i> W. and G.S. West			F									
<i>Navicula stauropteroides</i> Fritsch						R						R
<i>Navicula seminulum</i> Grunow					A	A				F		F
<i>Nacinnula</i> sp.							R			R		F
<i>Denticula tenuis</i> Kutzing			R		C	R						
<i>Biddulphia</i> sp.						R				R		
<i>Uroglena</i> sp.					C	A		C		A		A

\* Abbreviations: A, abundant; C, common; F, few; R, rare.

TABLE 2 (Continued)  
POPULATIONS OF MELT-WATER POOLS ON CLARK PENINSULA AND AN UNNAMED ISLET, ANTARCTICA

ORGANISMS	POOL NUMBER											
	1	2	3	4	5	6	7	8	9	10	11	12
FLORA (Continued)												
CYANOPHYCEAE												
<i>Nodularia spumigena</i> Mertens					F*							
<i>Polycistus</i> sp.	A		A		A	A	A	A	R	R		A
<i>Lyngbya aeronginea-caerulea</i> (Kutzing)	A		C		A	C	A			A		
<i>Oscillatoria</i> sp. A	A	F	A	C	A	C		C	R		R	A
<i>Oscillatoria</i> sp. B	A	R		A	A	A		C	R			A
<i>Phormidium</i> sp.			C	A	C	C						A
<i>Schizothrix antarctica</i> Fritsch					R					A		
<i>Stauroneis antarctica</i> (Gran. and Angst.)				C	A	A		C				A
<i>Stauroneis</i> sp.				R	A							
<i>Nostoc longstaffi</i> Fritsch				C	A							
<i>Anabaena antarctica</i> Fritsch					A	F				C		
<i>Dactyloopsis antarctica</i> Fritsch					A							
FAUNA												
<i>Amoeba terricola</i> Greeff.												
<i>Stylonychia</i> sp.					A	C	C	C		C		C
? <i>Philodina</i> sp.			R	C								
<i>Habrotrocha</i> sp.				R								
<i>Brachionus quadridentatus</i> Hermann			F				R					
<i>Brachionus calyciflorus</i> Pallas			F	F			F					
<i>Macrobiotus</i> sp.							C					
<i>Cyclopoid copepoda</i>				R								

\* Abbreviations: A, abundant; C, common; F, few; R, rare.

have been collected in New Zealand is 10° C. As far as Dr. Russell knows this is the first time members of the genus *Brachionus* have been collected in polar waters.

The presence of *Brachionus* and other cosmopolitan genera in Antarctic assemblages raises the question of how they were introduced into the south polar region. Several means of distribution have been suggested:

1. *Continental association.* According to Kuonen (1950) there are several theories to account for the dispersal of plants and animals to (and from) Antarctica. Of these the continental drift hypothesis of Wegener (1924) appears to be the most popular. It postulates the Paleozoic existence of Gondwanaland from which, in the early Mesozoic, the continents of the southern hemisphere broke off and drifted apart. Stille (1944) and others deduce from seismic evidence that much of the area between Antarctica and Australia is a slumped continent. Hedley (1911) and his school believe in an ancient isthmian link between Australia, Antarctica, and South America. Hedley's thesis is invoked by Du Rietz (1940) and others to explain the bipolar distribution of common plants.

2. *Dispersal by the wind.* Allee et al. (1950) mention "plankton of the air" consisting of dessicated animals and plants, cysts, eggs, etc., which drift with the air currents, sometimes as high as the stratosphere. Upon falling to earth, they resume normal activity where the environment is favorable.

3. *Distribution by birds.* According to Hesse et al. (1958) water birds are transportation media for aquatic microorganisms. Not only may biota be carried externally but cysts and eggs may be eaten and excreted. Eklund (1961) says skuas were often seen to drink at fresh-water ponds. According to Stead (1932), *Catacracta antarctica* (*C. skua lonnbergi*) range from New Zealand to Antarctica.

Considering the application of the foregoing agencies to Clark Peninsula pools, that of continental association can be discarded for two reasons. First, there is no fossil evidence that non-marine fish, amphibians, reptiles, or mammals were ever present in Antarctica. Second, and most cogent, the pools were submerged, in Recent time, in the sea. While distribution

by the wind may play a role in dispersion of fresh-water biota, the dominant one is likely that of birds. Skua gulls are capable of transporting organisms from a pool in New Zealand to one in the Antarctic.

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# Nomenclatural Notes on Hawaiian Myrsinaceae

ROBERT L. WILBUR<sup>1</sup>

THE HAWAIIAN REPRESENTATIVES of the genus *Myrsine* L., including those entities sometimes assigned to the segregated *Suttonia* A. Rich. and *Rapanea* Aubl., were most recently revised by Hosaka (Occ. Pap. Bishop Mus. 16:25–76, 1940). In this paper 25 Hawaiian taxa were recognized and 21 of these were considered species. Hosaka's account appears to be a very significant milestone in elucidating a difficult group of Hawaiian trees and shrubs. Unfortunately for the sake of stability, the names applied to three of the species and one variety are not in accord with the International Code. The four required new combinations or names and the synonymy of these taxa are presented below.

1. *Myrsine Hosakae* nom. nov.

*Suttonia angustifolia* Mez, Pflanzenreich. 9 (IV. 236):337, 1902.

*Myrsine angustifolia* (Mez) Hosaka, Occ. Pap. Bishop Mus. 16:42, 1940, non D. Dietr., Syn. Pl. 1:619. 1839.

The name of this species is of course intended as a memorial to the late Edward Y. Hosaka, student of the Hawaiian vegetation and flora, whose efforts to delineate the Hawaiian taxa of *Myrsine* resulted in a most useful publication.

2. *Myrsine Meziana* (Lévl.) comb. nov.

*Myrsine Gaudichaudii* A.DC. forma *acuminata* Wawra, Flora 57:524, 1874.

*Suttonia Meziana* Lévl., Repert. Sp. Nov. 10:443, 1912.

*Myrsine Fosbergii* Hosaka var. *acuminata* (Wawra) Hosaka, Occ. Pap. Bishop Mus. 16:47, 1940.

Hosaka overlooked Léveillé's binominal, *Suttonia Meziana*, but cited one of its isotypes (Faurie 428) among the specimens examined. Unfortunately there may be some confusion in names between this species from Oahu and Molokai and *Myrsine Mezii* Hosaka from Kauai.

3. *Myrsine Meziana* (Lévl.) Wilb. var. *Fosbergii* (Hosaka) comb. nov.

*Myrsine Fosbergii* Hosaka, Occ. Pap. Bishop Mus. 16:46, 1940.

4. *Myrsine punctata* (Lévl.) comb. nov.

*Myrsine Sandwicensis* A.DC. var. *lanceolata* Wawra, Flora 57:526, 1874.

*Myrsine lanceolata* (Wawra) Heller, Minn. Bot. Stud. 9:873, 1897, non Wallich, 1829.

*Myrsine tenuifolia* Heller, l.c. invalid name, published in synonymy of *M. lanceolata*.

*Myrsine sandwicensis* A.DC. var. *punctata* Lévl., Repert. Sp. Nov. 10:157, 1911.

*Suttonia punctata* (Lévl.) Lévl., Repert. Sp. Nov. 10:443, 1912.

*Suttonia apodocarpa* Lévl., Repert. Sp. Nov. 10:444, 1912.

*Suttonia sandwicensis* (A.DC.) Mez var. *apodocarpa* (Lévl.) Rock, Indigenous Trees Haw. Is. 379, 1913.

*Suttonia lanceolata* (Wawra) Rock, Indigenous Trees Haw. Is. 379, 1913.

*Rapanea Rockii* Degener & Hosaka, Fl. Haw. 1939.

*Myrsine Rockii* (Degener & Hosaka) Hosaka, Occ. Pap. Bishop Mus. 16:50, 1940.

There appears to be no obstacle to using either of Léveillé's binomial epithets in *Myrsine* or *Rapanea* and hence Degener and Hosaka should have taken up one of them. Skottsberg (Acta Horti Gothob. 15:428, 1944) questioned their failure to adopt (Léveillé's *S. punctata*, but to my knowledge the necessary combination has not been made.

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## Revision of the Genus *Pandanus* Stickman, Part 20

### New Species from India and Thailand

HAROLD ST. JOHN<sup>1</sup>

THE FOLLOWING NEW SPECIES of *Pandanus* from India and Thailand are, all except one, based upon collections made by botanists other than the writer.

#### SPECIES FROM INDIA

##### Section *Rykia*

*Pandanus assamensis* sp. nov. (sect. *Rykia*).

Fig. 225

DIAGNOSIS HOLOTYPE: Caule 6–7 mm diametro brunneo lucido laevi, internodis 10–11 mm longis, foliis 28–30 cm longis 22–27 mm latis chartaceis supra viridibus infra pallidioribus 1-sulcatis 2-plicatis in sectione mediali cum 15–16 nervis parallelis secundariis ubique conspicuis in quaque media, nervis tertiis nullis, laminis infra cuneatis proxima basem 15–16 mm latis ligulatis ad apicem subiter in apice subulato 3 cm longo 0.5–0.7 mm lato contractis basi amplexicauli inermi sed ex 2.5–3 cm marginibus cum aculeis 1–2 mm longis 1.5–3 mm separatis rectis subulatis adscendentibus apicibus subulatis, midnervo infra ex 5–5.5 cm cum aculeis 2–2.5 mm longis 14–26 mm separatis subulatis reflexis basibus incrassatis, in sectione mediali marginibus cum aculeis 0.3–0.5 mm longis 1–8 mm separatis acicularibus adpresse adscendentibus, midnervo cum aculeis paucis 0.7–0.8 mm longis 20–25 mm separatis crassiter subulatis reflexis basibus latis, in apice caudato marginibus et midnervo infra cum aculeis 0.3–0.5 mm longis 0.2–1 mm separatis validis arcuatis subulatis adscendentibus; inflorescentia foeminea cum syncarpio terminali erecto solitario, pedunculo 8 cm longo 3 mm diametro 3-laterato supra crassiori et in apice 4 mm diametro cum bracteis paucis, syncarpio 3.5 cm longo 2.5 cm diametro

oblongo-ellipsoideo cum circa 720 drupis eis 11–12 mm longis 2 mm latis et crassis 5–6-angulatis corpore 7–8 mm longo oblongo-oblanceoloideo, pileo cum basi 1.5–2 mm alto semiellipsoideo laevi vel minime papilloso, stylo 5–6 mm longo graciliter subulato in basi valde reflexo, drupis superis cum stylis terminalibus illis latioribus cum stylis lateralibus, stigmate 4–5 mm longo lineari proximo brunneo papilloso fere ad apicem extento, endocarpio supra-mediali lateribus 0.07 mm crassis cartilagineis stramineis, mesocarpio apicali parvo medullosa, mesocarpio basali in lateribus fibroso intra carnoso.

DIAGNOSIS OF HOLOTYPE: Stem 6–7 mm in diameter, brown, shining, smooth, the internodes 10–11 mm long; leaves 28–30 cm long, 22–27 mm wide, chartaceous, green above, pale green below, 1-ribbed, but 2-pleated, at midsection with 15–16 parallel secondary veins in each half, these conspicuous on both sides throughout, no tertiary cross veins, cuneate below and just above the base only 15–16 mm wide, ligulate, near the apex abruptly contracted to a subulate tip 3 cm long, this 0.5–0.7 mm wide, the base amplexicaul and unarmed, but starting 2.5–3 cm up the margins with prickles 1–2 mm long 1.5–3 mm apart, straight subulate, ascending, reddish tipped; the midrib below beginning at 5–5.5 cm with prickles 2–2.5 mm long, 14–26 mm apart, subulate, reflexed, heavy based; at midsection the margins with prickles 0.3–0.5 mm long, 1–8 mm apart, acicular, appressed ascending; the midrib below with a few prickles 0.7–0.8 mm long, 20–25 mm apart, stout subulate, broad based, reflexed; on the caudate apex the margins and midrib below with prickles 0.3–0.5 mm long, 0.2–1 mm apart, stout, arcuate subulate, ascending; pistillate inflorescence with one terminal, erect, solitary syncarp; peduncle 8 cm long, 3 mm in diameter, 3-sided, few bracted,

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thickening upwards and near the apex 4 mm in diameter; syncarp 3.5 cm long, 2.5 cm in diameter, oblong-ellipsoid, bearing about 720 drupes, these 11–12 mm long, 2 mm wide and thick, 5–6-angled, the body 7–8 mm long, oblong-oblancoeloid; pileus with its base 1.5–2 mm high, semiellipsoid, the surface smooth or slightly papillose; style 5–6 mm long, slender subulate, bent at base and sharply reflexed, the upper drupes with nearly terminal styles, the lower ones with styles lateral in attachment; stigma 4–5 mm long, linear, proximal, brown, papillose, running almost to the stigma tip; endocarp in lower  $\frac{1}{3}$ , the walls 0.07 mm thick, cartilaginous, stramineous; seed 2.5 mm long, ellipsoid; apical mesocarp sparse, pithy; basal mesocarp fibrous up the margins, fleshy within.

HOLOTYPE: India, Assam, Kambang, plains, May 1888, *L. Wray, Jr.* 1,939 (SING). Isotype (CAL).

DISCUSSION: *P. assamensis* is a member of section *Rykia*, as is the most closely related species, *P. Scortechinii* Martelli, of Perak, Malaya. The new holotype was included among the specimens cited by Martelli when he published the latter species. Later, he typified his species by a collection from Perak, Malaya, and omitted the collection from Assam. One of these is made the basis of the species here described as new. *P. Scortechinii* has the style 4–5 mm long, subulate from a broad, compressed base, terminal and ascending; stigma 2.5–3 mm long; endocarp in lower  $\frac{1}{3}$ ; stem near the apex 13 mm in diameter; leaf with the caudate tip 1.3 mm wide, the marginal prickles near the base 3–6 mm apart, the nearby midrib below with prickles 0.5–1 mm long, and at midsection the midrib unarmed. *P. assamensis* has the style 5–6 mm long, slender subulate, the apical drupes with terminal styles, the middle and lower ones with lateral styles; stigma 4–5 mm long; endocarp in lower  $\frac{1}{3}$ ; stem near the apex 6–7 mm in diameter; leaf with the caudate tip 0.5–0.7 mm wide, the marginal prickles near the base 14–26 mm apart,

the nearby midrib below with prickles 2–2.5 mm long, and at midsection the midrib below with prickles 0.7–0.8 mm long.

#### SPECIES FROM THAILAND

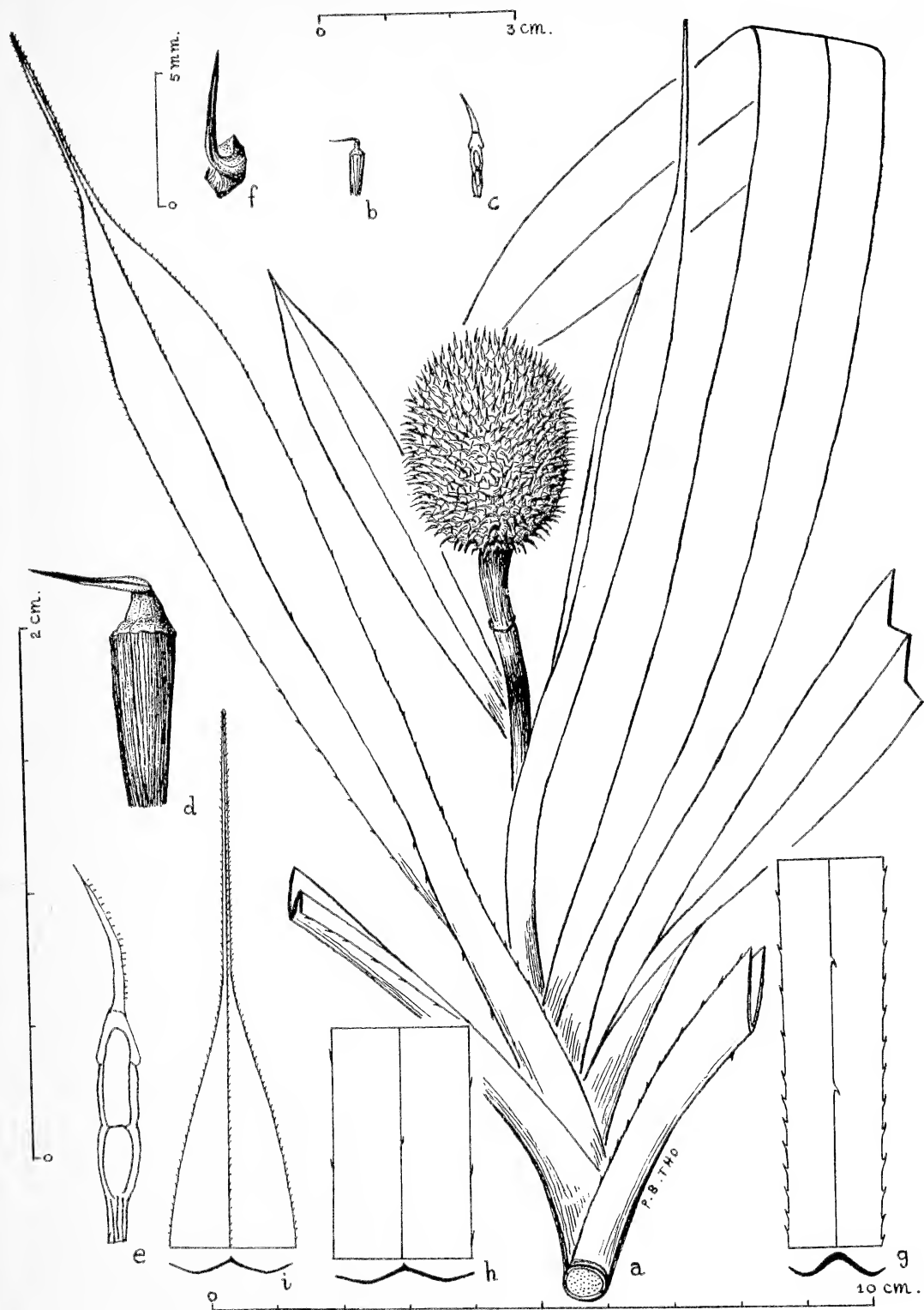
##### Section *Acrostigma*

*Pandanus retroaculeatus* sp. nov. (sect. *Acrostigma*).

Fig. 226

DIAGNOSIS HOLOTYPE: Planta 2 m alta, foliis circa 64 cm longis 2 cm latis supra viridibus infra pallide viridibus chartaceis excepta in basi subcoriacea supra midnervum sulcatis 2-plicatis ligulatis sed in dm ultimo in apice subulato diminuentibus (apex deest) in sectione mediali cum 28 nervis parallelis secundariis in quoque latere ubique prominentibus ad apicem nervis tertiis obliquis remotis evidentis basi amplexicauli et inermi conspicue nervosa ex 6 cm marginibus cum aculeis 1.5–2 mm longis 2–5 mm separatis subulatis luteis inferis divergentibus, midnervo infra ex 9 cm cum aculeis 3.5–5 mm longis 5–12 mm separatis crassiter subulatis valde reflexis basi incrassata, in sectione mediali marginibus cum aculeis 0.8–1 mm longis 2–5 mm separatis subulatis adscendentibus, midnervo angusto et elevato cum aculeis 0.5–0.8 mm longis 3–5 mm separatis subulatis adscendentibus, proxima apicem marginibus cum serrulis 0.2–0.4 mm longis 0.5–1.5 mm separatis, midnervo infra cum serrulis 0.6–0.8 mm longis 2–3 mm separatis, in pagina supera ex medio ad apicem plicis binis cum aculeis 0.3–0.5 mm longis 1–3 mm separatis subulatis adscendentibus, inflorescentia foeminea erecta folioso-bracteata cum syncarpio solitario, pedunculo 13 cm longo 3–4 mm diametro 3-laterato, bracteis floraceis circa 9 luteis inferiore 7.5 cm longa 1 cm lata lineari-lanceolata marginibus mediae ultimae cum aculeis pallidis congestis 0.1–0.2 mm longis, syncarpio (immature) 2 cm longo 18 mm diametro ovoideo cum circa 288 drupis eis cum pileo 6–8 mm longo basi 3 mm alta 5-angulosa lanceoloidea laevi et cum sulca pro-

FIG. 225. *Pandanus assamensis* St. John, from holotype. *a*, fruiting branch, lateral view,  $\times 1$ ; *b*, drupe, lateral view,  $\times 1$ ; *c*, drupe, longitudinal median section,  $\times 1$ ; *d*, drupe, lateral view,  $\times 4$ ; *e*, drupe, longitudinal median section,  $\times 4$ ; *f*, drupe, style, and stigma, apical view,  $\times 4$ ; *g*, leaf base, lower side,  $\times 1$ ; *h*, leaf middle, lower side,  $\times 1$ ; *i*, leaf apex, lower side,  $\times 1$ .





fundo ex stigmatē descendenti, stylo 3–5 mm longo subulato subarcuato vel recto osseoso subluteo, stigmatē 3.5–5 mm longo lineari distali obscure brunneo papilloso, corpore 2.5–3 mm longo immaturo.

**DIAGNOSIS OF HOLOTYPE:** Plant 2 m tall; leaves about 64 cm long, 2 cm wide, green above, pale green below, towards the base subcoriaceous, the rest chartaceous, sulcate above the midrib, 2-pleated, ligulate but in the last dm tapering to a subulate apex (the tip lacking in ours), at midsection with 28 parallel secondary veins, these prominent throughout, towards the apex the remote oblique tertiary cross veins visible, the base amplexicaul and unarmed, prominently veiny, beginning at 6 cm the margins with prickles 1.5–2 mm long, 2–5 mm apart, subulate, yellowish, the lowest ones divergent, the midrib below beginning at 9 cm with prickles 3.5–5 mm long, 5–12 mm apart, stout subulate, sharply reflexed, the base thickened; at midsection the margins with prickles 0.8–1 mm long, 2–5 mm apart, subulate, ascending; the midrib below narrow and raised, with prickles 0.5–0.8 mm long, 3–5 mm apart, subulate, ascending; near the tip the margins with serrulations 0.2–0.4 mm long, 0.5–1.5 mm apart; the midrib below with serrulations 0.6–0.8 mm long, 2–3 mm apart; on the upper surface from the middle to the tip the pleats with prickles 0.3–0.5 mm long, 1–3 mm apart, subulate, ascending; pistillate inflorescence erect, leafy bracted, bearing one syncarp; peduncle 13 cm long, 3–4 mm in diameter, 3-sided; floral bracts about 9, yellow, the lowest 7.5 cm long, 1 cm wide, linear-lanceolate, the margins of the outer half with pale, crowded prickles 0.1–0.2 mm long; syncarp (young) 2 cm long, 18 mm in diameter, ovoid, bearing about 288 drupes, these with pileus 6–8 mm long, its base 3 mm high, 5-angled, lanceoloid, smooth, with a deep furrow continuing down from the stigma; style 3–5 mm long, subulate, slightly arcuate or straight, bony, yellowish; stigma 3.5–5 mm long, linear, distal, dark brown, papillose; body 2.5–3 mm

long, too immature to reveal its structure.

**HOLOTYPE:** Thailand, Ronpibun Hill, Nakawn Srichamrat, jungle, 2,000 ft alt, *Eryl Smith* 485 (BK).

**DISCUSSION:** *P. retroaculeatus* is a member of the section *Acrostigma*, as is its closest relative, *P. Toinu* St. John, also of Thailand, a species with the pileus 5 mm long; stigma 2–2.5 mm long; stems 15 cm tall; leaves 14 mm wide, firm chartaceous, at midsection with 19–20 parallel secondary veins in each half, the tertiary cross veins visible nearly throughout, beginning at 5 cm from the base the margins with prickles 1–1.5 mm long, 2–5 mm apart, lance-deltoid, and flat. *P. retroaculeatus* has the pileus 6–8 mm long; stigma 3.5–5 mm long; stems 1.5 m tall; leaves 20 mm wide, chartaceous except for the subcoriaceous base, at midsection with 28 parallel secondary veins in each half, the tertiary cross veins oblique, remote, visible towards the apex, beginning at 6 cm from the base the margins with prickles 1.5–2 mm long, 2–5 mm apart, and stout.

The new epithet is from the Latin *retorsus*, backward, and *aculeatus*, with prickles, and it is given with allusion to the strong, retrorse prickles of the midrib.

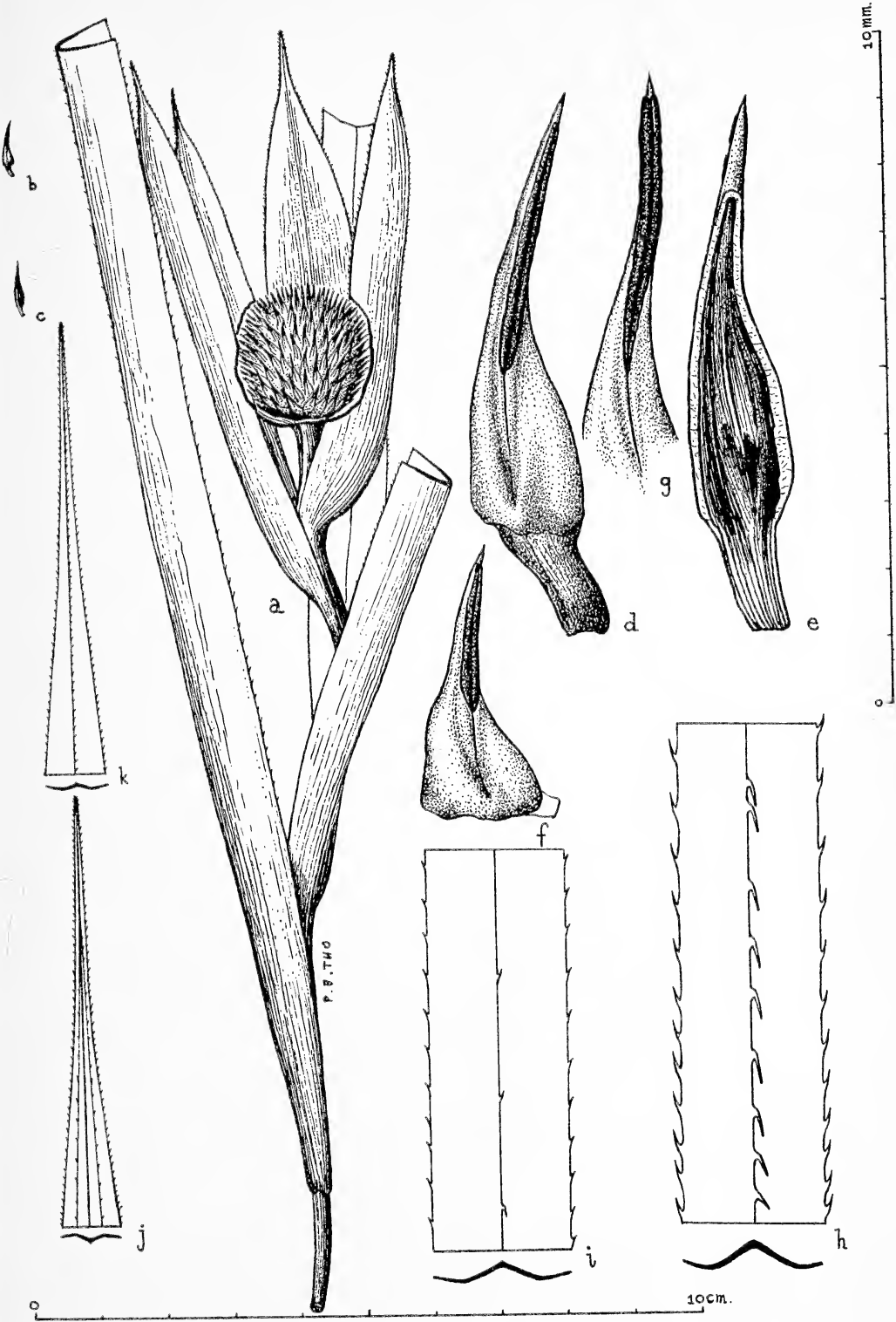
*Pandanus Toinu* sp. nov. (sect. *Acrostigma*).

Fig. 227

NOM. VERN.: "tôi nu."

**DIAGNOSIS HOLOTYPI:** Planta erecta aggregata, caulibus 15 cm altis 8 mm diametro, foliis 72 cm longis 14 mm latis firme chartaceis supra viridibus infra pallide viridibus 1-sulcatis 2-plicatis in sectione M-formatis ligulatis in apice in 8 cm ultimis sensim diminuentibus in apice subulato 1 cm longo in sectione mediali cum 19–20 nervis parallelis secundariis in quaque media eis ubique evidentis et reticulis oblongis elongatis formantibus in media ultima plicis supra cum subulato-serrulis 0.5–0.9 mm longis 2–4 mm separatis basi amplexicauli inermi sed nervis longitudinalibus prominentissimis ex 5

FIG. 226. *Pandanus retroaculeatus* St. John, from holotype. *a*, fruiting branch, lateral view,  $\times 1$ ; *b*, *c*, drupe, lateral view,  $\times 1$ ; *d*, drupe, lateral view  $\times 10$ ; *e*, drupe, longitudinal median section,  $\times 10$ ; *f*, *g*, pileus, style, and stigma, lateral view,  $\times 10$ ; *h*, leaf base, lower side,  $\times 1$ ; *i*, leaf middle, lower side,  $\times 1$ ; *j*, leaf apex, upper side,  $\times 1$ ; *k*, leaf apex, lower side,  $\times 1$ .



cm marginibus cum aculeis 1–1.5 mm longis 2–5 mm separatis lanceo-deltoides complanatis luteis adscendentibus, midnervo infra ex 5.5 cm cum aculeis 0.7–1.5 mm longis 2–8 mm separatis subulato-conicis infimis erectis alteris reflexis, in sectione mediali marginibus cum subulato-serrulis 0.7–0.9 mm longis 2–3 mm separatis, midnervo infra cum serrulis 0.5 mm longis 4–8 mm separatis vel nullis, ad apicem marginibus et midnervo infra cum serrulis 0.1 mm longis 1–2 mm separatis, inflorescentia foeminea erecta foliosa cum syncarpio solitario, pedunculo 8 cm longo 4 mm diametro trigono, syncarpio (immaturum) 2 cm longo 18 mm diametro ovoideo-subglobose cum circa 240 drupis eis immaturis 7–8 mm longis, pileo 5 mm longo obliquiter lanceoloideo proxime curvato osseoso luteo basi 2 mm alta 1.7–2 mm lata obliquiter pyramidalis prominente 5-angulosa glauca, stylo 3 mm longo crassiter subulato arcuato lucido subtereto, stigmatibus 2–2.5 mm longo late lineari cinnamomum-brunneo papilloso subterminali, corpore 2.5–3 mm longo oblanceoloideo immaturo contracto.

**DIAGNOSIS OF HOLOTYPE:** Plant erect, forming tufts; stems about 15 cm tall, 8 mm in diameter; leaves 72 cm long, 14 mm wide, firm, chartaceous, green above, pale green below, with one central furrow, 2-pleated, in section M-shaped, ligulate, at tip gradually narrowed in the last 8 cm to a 1 cm subulate apex, at midsection with 19–20 parallel secondary veins in each half, these prominent throughout, the tertiary cross veins visible nearly throughout, forming a network with the meshes elongate oblong, on the outer half the pleats on the upper surface with subulate-serrulations 0.5–0.9 mm long, 2–4 mm apart, the base amplexicaul, unarmed, but the longitudinal veins very prominent, beginning at 5 cm the margins with prickles 1–1.5 mm long, 2–5 mm apart, lance-deltoid, flat, yellow, ascending; the midrib below beginning at 5.5 cm with prickles 0.7–1.5 mm long, 2–8 mm apart, subulate conic, the lowest erect, the others

becoming reflexed; at midsection the margins with subulate-serrulations 0.7–0.9 mm long, 2–3 mm apart; the midrib below with serrulations 0.5 mm long, 4–8 mm apart, or none; near the tip the margins and midrib below with serrulations 0.1 mm long, 1–2 mm apart; pistillate inflorescence erect, leafy, bearing a single syncarp; peduncle 8 cm long, 4 mm in diameter, trigonous; syncarp (immature) 2 cm long, 18 mm in diameter, ovoid-subglobose, bearing about 240 drupes, these (immature and the body little developed) 7–8 mm long; pileus 5 mm long, obliquely lanceoloid, proximally curved, bony, yellow, the base 2 mm high, 1.7–2 mm wide, obliquely pyramidal, prominently 5-angled, glaucous; style 3 mm long, thick subulate, arcuate, shining, subterete; stigma 2–2.5 mm long, broad linear, cinnamon-brown, papillose, reaching quite to the tip; body 2.5–3 mm long, oblanceoloid, shrunken, immature.

**HOLOTYPE:** Thailand, Padang Besar, 50 m alt, light evergreen forest, Dec. 25, 1927, *A. F. G. Kerr* 13,639 (BK).

**DISCUSSION:** *P. Toinu* is a member of the section *Acrostigma*, as is its closest relative, *P. similis* Craib, of Thailand, a species with the pileus 5 mm wide, the base hemispheric; style flat; leaves 1 m long, 14–19 mm wide, near the base the midrib with prickles 1.5–2 mm long, 15–20 mm apart, reflexed, at midsection the margins with white serrations 0.4–0.5 mm long, and 3–6 mm apart. *P. Toinu* has the pileus 1.7–2 mm wide, the base obliquely pyramidal; style subterete; leaves 72 cm long, 14 mm wide, near the base the midrib with prickles 0.7–1.5 mm long, 2–8 mm apart; at midsection the margins with yellow subulate-serrulations 0.7–0.9 mm long, and 2–3 mm apart.

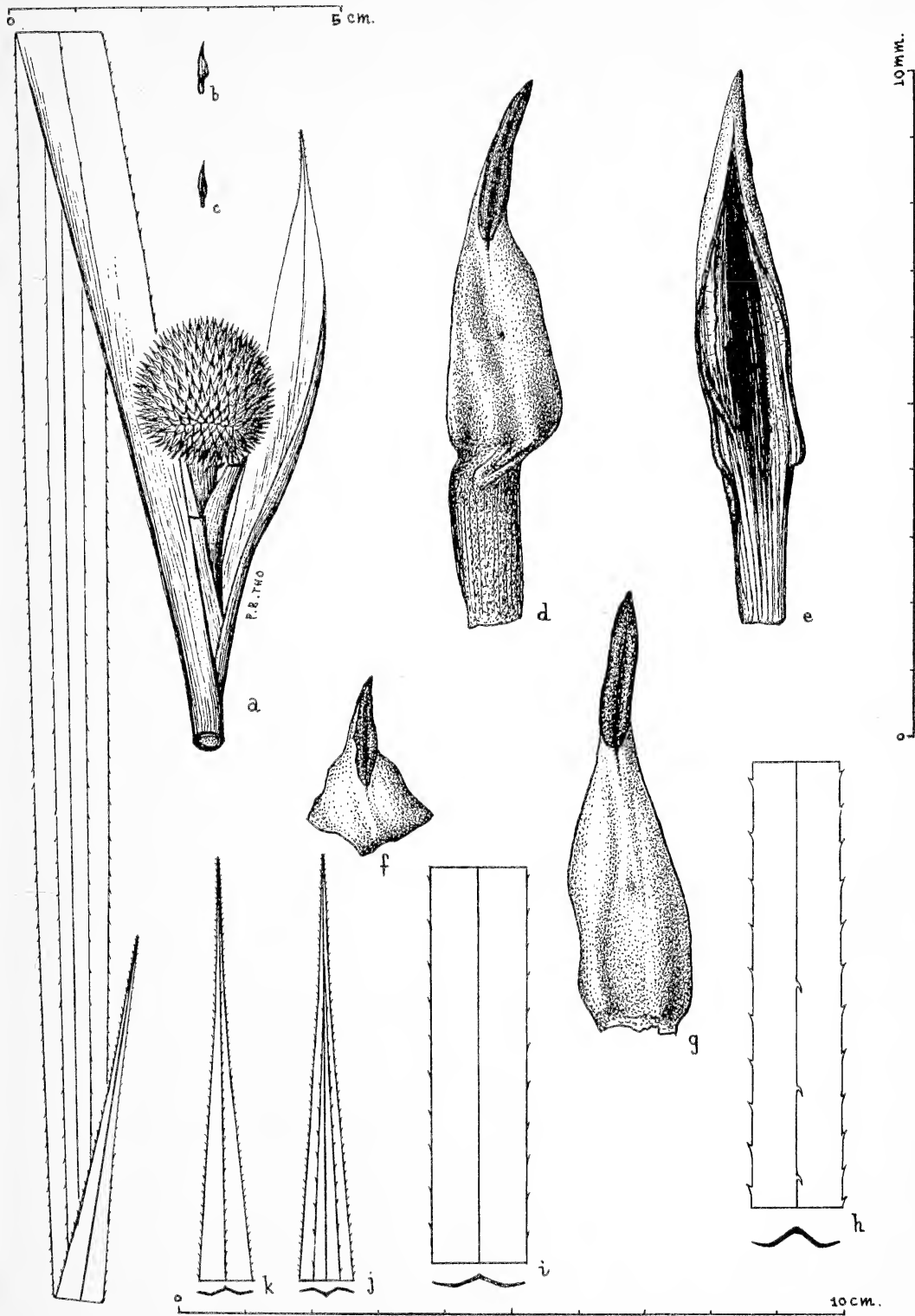
The specific epithet is the vernacular name of the species, used as a noun in apposition.

#### Section *Rykia*

*Pandanus acaulescens* sp. nov. (sect. *Rykia*).

Fig. 228

FIG. 227. *Pandanus Toinu* St. John, from holotype. *a*, fruiting branch, lateral view,  $\times 1$ ; *b*, *c*, drupe, lateral view,  $\times 1$ ; *d*, drupe, lateral view,  $\times 10$ ; *e*, drupe, longitudinal median section,  $\times 10$ ; *f*, *g*, style, and stigma, lateral view,  $\times 10$ ; *h*, leaf base, lower side,  $\times 1$ ; *i*, leaf middle, lower side,  $\times 1$ ; *j*, leaf apex, upper side,  $\times 1$ ; *k*, leaf apex, lower side,  $\times 1$ .

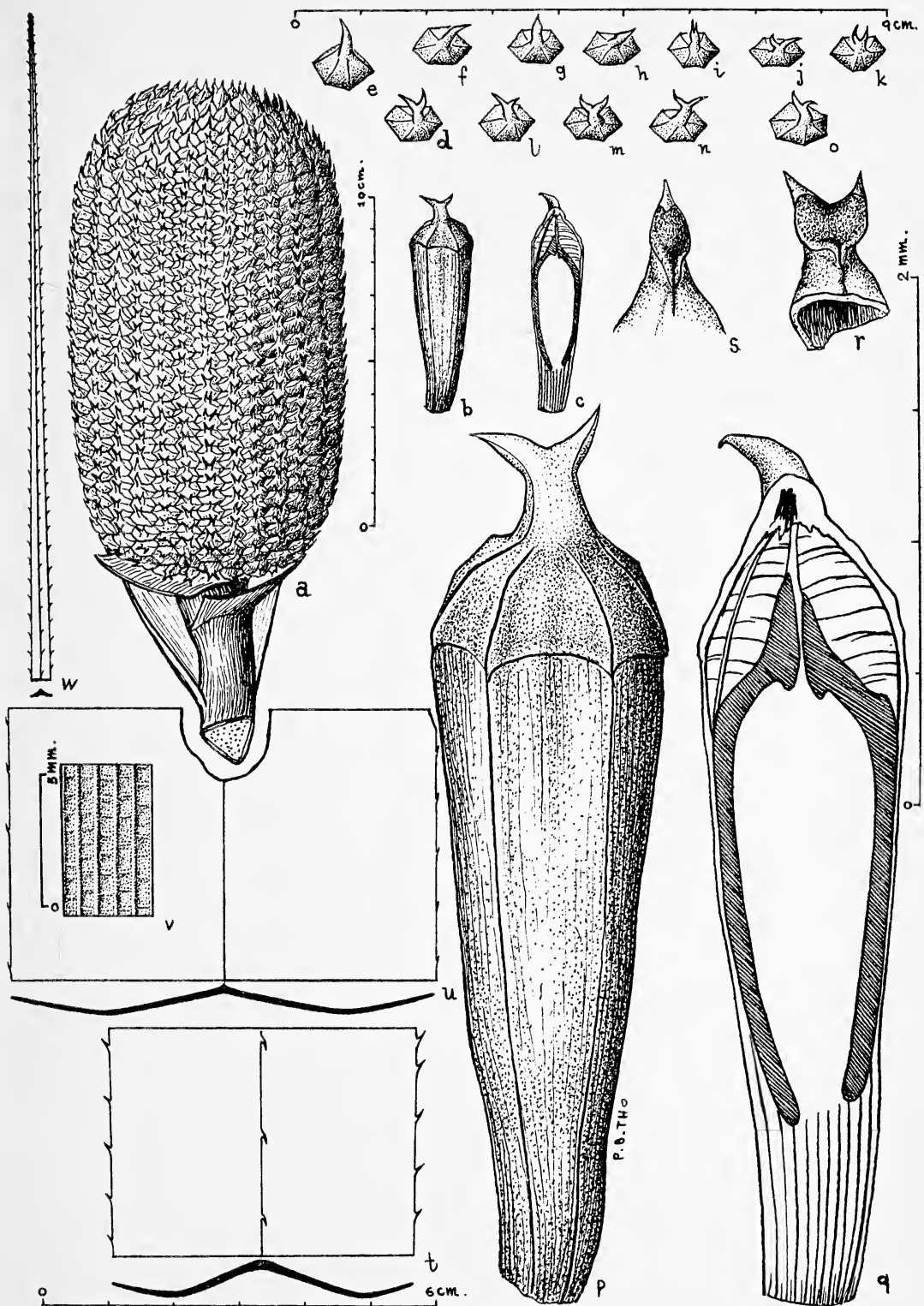


DIAGNOSIS HOLOTYPE: Planta acaulescens aggregata, foliis 2.54–3.5 m longis circa mediam 6.1 cm latis proxima basem 4 cm latis subtiliter coriaceis supra midnervum late sulcatis 2-plicatis in sectione mediali cum 49 nervis parallelis secundariis in quaque media nervis tertiis in media ultima conspicuis et reticulis quadratis formantibus lamina ligulata in apice trigono subulato 15 cm longo diminuentibus eo in puncto 10 cm ex apice 1.5 mm lato basi amplexicauli inermi crassa lucida rubro-brunnea, marginibus ex 16 cm cum aculeis 1.5–2.5 mm longis 5–10 mm separatis subulatis pallidis adscendentibus, midnervo infra ex 14 cm cum aculeis 2–3 mm longis 11–18 mm separatis arcuatis subulatis recurvatis per 16 cm extentis deinde ad  $\frac{1}{4}$  ultima inermi, in sectione mediali marginibus cum serrulis 0.7–1 mm longis 4–11 mm separatis, in apice subulato marginibus et midnervo infra cum serrulis 0.6–1 mm longis 1–4 mm separatis, inflorescentia foeminea erecta cum syncarpio solitario, pedunculo 56 cm longo trigono subclavato in apice 15 mm diametro media ultima folioso-bracteato, bracteis syncarpium includentibus interioribus marcescentibus et in stigmatibus affixis, bracteis superis 17 cm longis 6 cm latis marginibus superis et midnervo infra serrulatis, syncarpio 14.5 cm longis 9.3 cm diametro ellipsoideo 3-laterato cum circa 696 drupis in lineis verticalibus, drupis 32–33 mm longis 7–10 mm latis 6–10 mm crassis obscure viridibus crassiter cuneatis 6-angulosis parte  $\frac{1}{5}$  supera libera corpore 25–26 mm longo lateribus planis, pileo cum basi 4–5 mm alta subrotundata-pyramidalis exlucida, stylo 4–6 mm longo longiter cornuformi osseoso mahogany-brunneo lucido infra tereto supra complanato valde proxime curvato plerumque  $\frac{1}{3}$ – $\frac{2}{5}$  bifido ramis plerumque divergentibus (stylo druparum terminalium subulato integro), stigmatibus 3–3.5 mm longo lanceolato proximo brunneo papilloso, endocarpio mediali elliptico-oblancoideoso osseoso brunneo lateribus lateralibus 1 mm cras-

sis intra laevi et lucido apice in projectione lanceo-subulato extenso, semine 13 mm longo oblanceo-ellipsoideo, mesocarpio apicali cavenoso cum membranis medullois transversis albis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Acaulescent, tufted plant; leaves 2.54–3.5 m long, 6.1 cm wide a little beyond the middle, near the base 4 cm wide, thin coriaceous, broadly furrowed above the midrib, 2-pleated, at midsection with 49 parallel secondary veins in each half, the tertiary cross veins conspicuous in the outer half, making a reticulum of squarish meshes, blade ligulate, tapering to a 15 cm trigonous, subulate tip, this 10 cm down 1.5 mm wide, the base amplexicaul, unarmed, thick, shining, reddish brown, the margins beginning at 16 cm with prickles 1.5–2.5 mm long, 5–10 mm apart, subulate, pale, ascending; the nearby midrib below beginning at 14 cm with prickles 2–3 mm long, 11–18 mm apart, arcuate, subulate, recurved, these extending for only 16 cm, then the midrib unarmed till the last quarter; at midsection the margins with serrulations 0.7–1 mm long, 4–11 mm apart, on the subulate apex the margins and midrib below with serrulations 0.6–1 mm long, 1–4 mm apart; pistillate inflorescence erect, with 1 syncarp; peduncle 56 cm long, trigonous, subclavate, at apex 15 mm in diameter, the upper half leafy bracted, the bracts enclosing the syncarp and the inner ones becoming marcescent and impaled on the sharp stigmas; upper bracts 17 cm long, 6 cm wide, their upper margins and midrib serrulate; syncarp 14.5 cm long, 9.3 cm in diameter, ellipsoid, 3-sided, bearing in vertical rows about 696 drupes, these dark green, 32–33 mm long, 7–10 mm wide, 6–10 mm thick, cuneate, 6-angled, upper  $\frac{1}{5}$  free, the body 25–26 mm long, its sides flat; pileus with the base 4–5 mm high, slightly rounded pyramidal, dull; style 4–6 mm long, hornlike, bony, mahogany-brown, shining, terete below, flattened above, sharply proximally curved, mostly

FIG. 228. *Pandanus acaulescens* St. John, from holotype. *a*, syncarp, lateral view,  $\times \frac{1}{2}$ ; *b*, drupe, lateral view,  $\times 1$ ; *c*, drupe, longitudinal median section,  $\times 1$ ; *d*, *i*, *j*, *k*, *l*, *m*, *n*, *o*, lateral drupes, apical view,  $\times 1$ ; *e*, *f*, *g*, *h*, apical drupes, apical view,  $\times 1$ ; *p*, drupe, lateral view,  $\times 4$ ; *q*, drupe, longitudinal median section,  $\times 4$ ; *r*, style and stigma of lateral drupe, lateral view,  $\times 4$ ; *s*, style and stigma of apical drupe, lateral view,  $\times 4$ ; *t*, leaf base, lower side,  $\times 1$ ; *u*, leaf middle, lower side,  $\times 1$ ; *v*, secondary and tertiary venation of leaf middle, lower side,  $\times 4$ ; *w*, leaf apex, lower side,  $\times 1$ .



bifid  $\frac{1}{3}$ – $\frac{2}{5}$  way, the forks mostly divergent (the apical drupes with the style simple, subulate); stigma 3–3.5 mm long, lanceolate, on the proximal face of the lobes, united below, brown, papillose; endocarp median, elliptic-oblancooid, bony, brown, the lateral walls 1 mm thick, the inner surface smooth, shining, the apex prolonged upwards into a lance-subulate projection; seed 13 mm long, oblance-ellipsoid; apical mesocarp cavernous, with transverse, white, medullary membranes; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Thailand, Chiangmai, Tat Noi, common in dry waterway, 900 m alt, tufted plant, no stems, 19 April 1960, *Tem Smitinand* 6,746 (BKF).

**DISCUSSION:** *P. acaulescens* is a member of the section *Rykia*, as is its closest relative, *P. penetrans* St. John, a species found in the same general locality, and one which has the infructescence pendent; syncarp 12 cm in diameter; drupes 33–35 mm long, 9–11 mm wide, upper  $\frac{1}{4}$  free; pileus 12–15 mm high, the base oblance-pyramidal; style 7–8 mm long; endocarp submedian; leaves 5–5.6 cm wide near the base, at midsection with 43 parallel secondary veins in each half, at midsection the margins with prickles 1.5–2.5 mm long, 13–22 mm apart, subulate, the nearby midrib below with prickles 3.5–5 mm long, 38–70 mm apart, stout subulate, reflexed; tree up to 9 m tall, 8 cm in diameter, the bark with ascending adventitious rootlets. *P. acaulescens* has the infructescence erect; syncarp 9.3 cm in diameter; drupes 32–33 mm long, 7–10 mm wide, upper  $\frac{1}{5}$  free; pileus 8–11 mm high, the base slightly rounded pyramidal; style 4–6 mm long; endocarp median; leaves 4 cm wide near the base, at midsection with 49 parallel secondary veins in each half, at midsection the margins with serrulations 0.7–1 mm long, 4–11 mm apart, the nearby midrib

below unarmed; and the plant acaulescent.

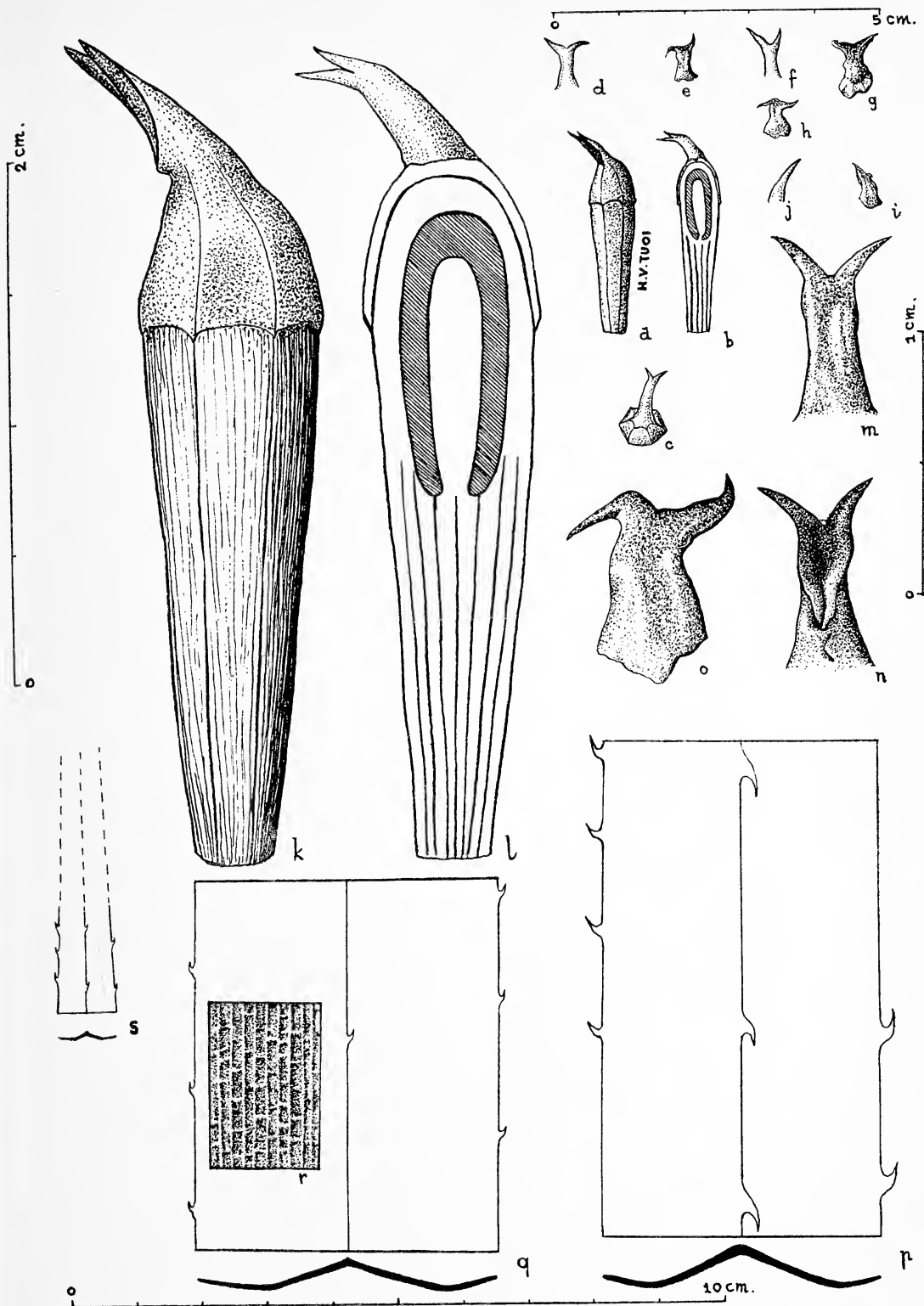
The new epithet is the Latin *acaulescens*, without a stem, and is here given as a descriptive name.

*Pandanus ligulatus* sp. nov. (sect. *Rykia*).

Fig. 229

**DIAGNOSIS HOLOTYPE:** Truncus 3 m altus, foliis 3.95 m et plus longis 4 cm latis subcoriaceis apparente pallide viridibus supra midnervum late sulcatis 2-plicatis ligulatis apice perditio, in sectione mediali cum 46 nervis parallelis secundariis in quoque dimidio ad apicem praecipue infra nervis tertiis conspicuis et oblongos angustos formantibus basi amplexicauli et inermi cupraceo sed ex 13–18 cm marginibus cum spinis 4–4.5 mm longis 25–45 mm separatis crasse arcuato-subulatis adscendentibus brunneis, midnervo infra cum spinis simulantibus sed crassioribus et reflexis, in sectione mediali marginibus cum aculeis 2–2.5 mm longis 15–21 mm separatis subulatis adpresse adscendentibus apicibus brunneis, midnervo infra cum aculeis simulantibus adscendentibus sed 30–33 mm separatis, in apice marginibus cum subulato-serrulis 1–1.5 mm longis 3–5 mm separatis, midnervo infra cum serrulis simulantibus 8–12 mm separatis, infructescencia pendenti cum syncarpio solitario, pedunculo 70 cm longo 1.3 cm diametro trigono folioso-bracteato, bracteis superis 20 cm longis 5 cm latis foliaceis marginibus cum subulato-serrulis 0.5 mm longis 3–5 mm separatis, syncarpio 11 cm longo 7.5 cm diametro late ellipsoideo viridi, drupis 27–32 mm longis 6–8 mm latis 5–7 mm crassis oblongo-oblancooideis eis lateralibus et subbasalibus minime compressis (illis apicalibus parve majoribus et paucis cum stylo subulato integri arcuato), pileo 10–13 mm longo basi 4–7 mm alto anguste pyramidaliconico 5–6-anguloso minute papilloso, stylo 6–7 mm longo osseoso brunneo lucido supra mediam compresso prox-

FIG. 229. *Pandanus ligulatus* St. John, from holotype. *a*, drupe, lateral view,  $\times 1$ ; *b*, drupe, longitudinal median section,  $\times 1$ ; *c*, drupe apex, apical view,  $\times 1$ ; *d*, *e*, *f*, *g*, *h*, style and stigma of lateral drupes, lateral view,  $\times 1$ ; *i*, *j*, style and stigma of apical drupes, lateral view,  $\times 1$ ; *k*, drupe, lateral view,  $\times 4$ ; *l*, drupe, longitudinal median section,  $\times 4$ ; *m*, style, distal view,  $\times 4$ ; *n*, style and stigma, proximal view,  $\times 4$ ; *o*, style, distal view,  $\times 4$ ; *p*, leaf base, lower side,  $\times 1$ ; *q*, leaf middle, lower side,  $\times 1$ ; *r*, secondary and tertiary venation at middle, lower side,  $\times 4$ ; *s*, leaf apex, lower side,  $\times 1$ .





ime subarcuato  $\frac{1}{4}$ – $\frac{1}{3}$  bifido, furcis inaequalibus divergentibus, stigmatibus 4–5 mm longo in basi lanceolato bifido brunneo papilloso ad apices non extento, endocarpio in parte  $\frac{2}{5}$  supera 11 mm longo cylindrico osseoso lateribus 1 mm crassis, semine 7 mm longo sublineari, mesocarpio apicali parvo fibroso et meduloso, mesocarpio basali fibroso et carnoso.

**DIAGNOSIS OF HOLOTYPE:** Stem 3 m tall; leaves more than 3.95 m long, 4 cm wide, subcoriaceous, apparently pale green, broad channeled above the midrib, 2-pleated, ligulate, the apex lost but apparently acuminate, at midsection with 46 parallel secondary veins in each half, towards the tip especially below the tertiary cross veins conspicuous and forming narrowly oblong meshes, the base amplexicaul, unarmed, copper-colored, but beginning at 13–18 cm the margins with thorns 4–4.5 mm long, 25–45 mm apart, stout arcuate subulate, ascending, brown; the midrib below with thorns similar but stouter and reflexed; at midsection the margins with prickles 2–2.5 mm long, 15–21 mm apart, subulate, appressed ascending, brown-tipped; the midrib below with similar ascending prickles but 30–33 mm apart; near the apex the margins with subulate-tipped serrations 1–1.5 mm long, 3–5 mm apart; the midrib below with similar serrations 8–12 mm apart; infructescence pendulous, bearing a single syncarp; peduncle 70 cm long, 1.3 cm in diameter, trigonous, leafy bracted, the upper bracts 20 cm long, 5 cm wide, foliaceous, the marginal teeth 0.5 mm long, 3–5 mm apart, subulate-serrulate; syncarp 11 cm long, 7.5 cm in diameter, broadly ellipsoid, green; drupes 27–32 mm long, 6–8 mm wide, 5–7 mm thick, oblong-oblancooid, the lateral and subbasal ones little or not at all compressed, 5–6-angled (the apical ones slightly the larger and a few of them with an unbranched, arcuate, subulate style); pileus 10–13 mm long, its base 4–7 mm high, narrowly

pyramidal-conic, 5–6-angled, minutely papillose; the style 6–7 mm long, bony, brown, shining, compressed above the middle, gently arcuate proximally, bifid  $\frac{1}{4}$ – $\frac{1}{3}$  way, the forks subequal, divergent, often unequally so; stigma 4–5 mm long, lanceolate at base, bifid, not reaching the tips, brown papillose; endocarp in upper  $\frac{2}{5}$ , 11 mm long, cylindric, bony, pale, the lateral walls 1 mm thick; seed 7 mm long, almost linear; apical mesocarp sparse, fibrous and pithy; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Thailand, northeastern part, Loei, Phu Krading, common in evergreen forest by stream, 1,300 m alt, 24 Nov. 1958, *Tem Smitinand* 4,950 (BKF).

**DISCUSSION:** *P. ligulatus* is a member of the section *Rykia*, as is its closest relative the Thai species *P. penetrans* St. John, which species has the syncarp 14 cm long, 12 cm in diameter; drupes 33–35 mm long, 9–11 mm wide, 7–10 mm thick; base of the pileus 7–10 mm high; endocarp submedian; seed 13 mm long; leaves 2.7–2.9 m long, 5–5.6 cm wide, near the base the margins with prickles 3.5–4 mm long, 11–18 mm apart. *P. ligulatus* has the syncarp 11 cm long, 7.5 cm in diameter; drupes 27–32 mm long, 6–8 mm wide, 5–7 mm thick; base of the pileus 4–7 mm high; endocarp in the upper  $\frac{2}{5}$ ; seed 7 mm long; leaves 3.9 or more m long, 4 cm wide; and near the base the margins of the leaves with thorns 4–4.5 mm long, 25–45 mm apart.

The new epithet is the Latin adjective, *ligulatus*, strap-shaped, in reference to the ligulate leaf blades.

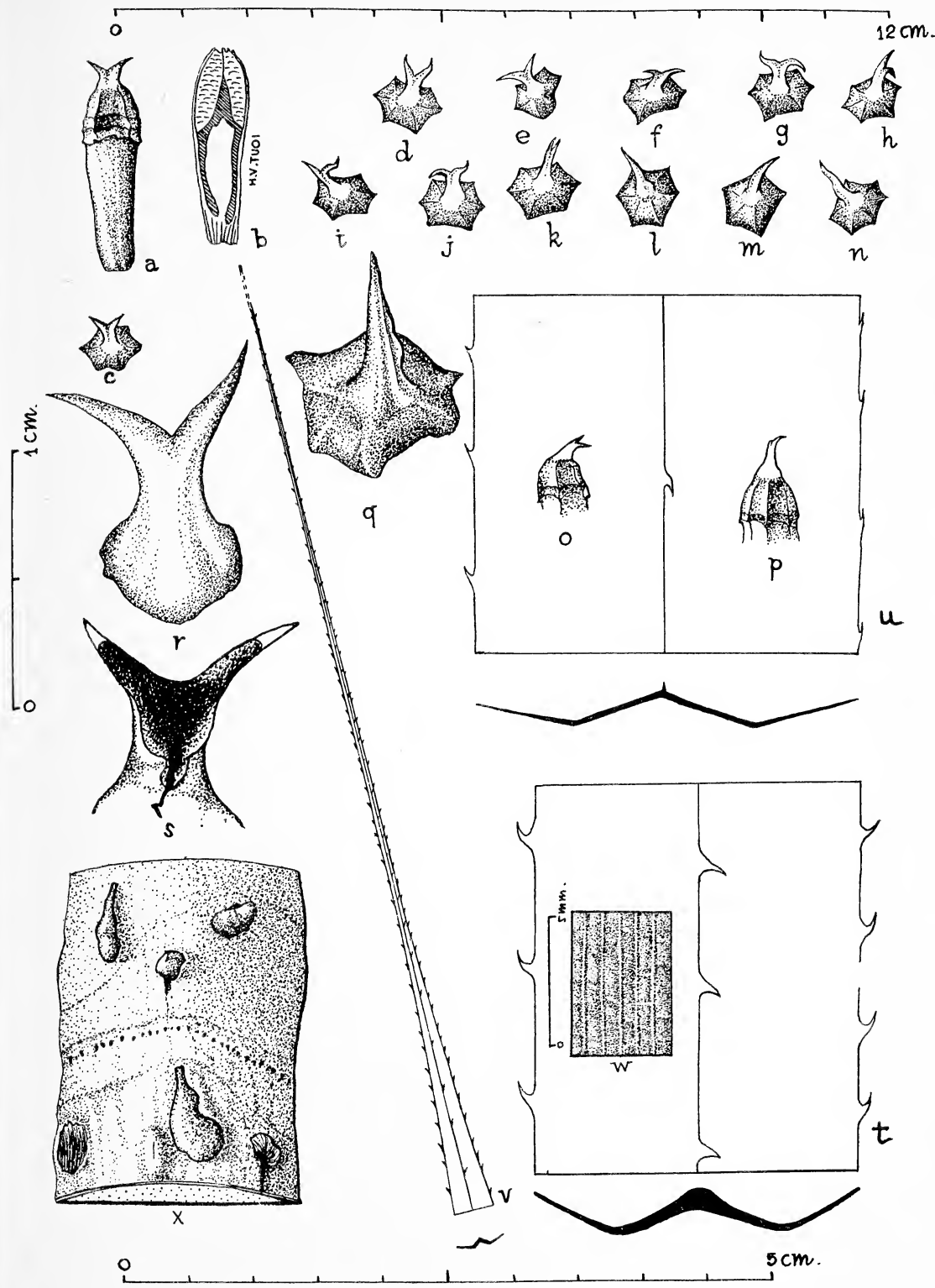
*Pandanus penetrans* sp. nov. (sect. *Rykia*).

Figs. 230, 231

NOM. VERN.: "toei."

**DIAGNOSIS HOLOTYPE:** Arbor 9 m alta 8 cm diametro, cortice brunneo cum radicillis 1 cm

FIG. 230. *Pandanus penetrans* St. John, from holotype. *a*, drupe, lateral view,  $\times 1$ ; *b*, drupe, longitudinal median section,  $\times 1$ ; *c*, *d*, *e*, *f*, *g*, *h*, *i*, *j*, *k*, lateral drupe and style, apical view,  $\times 1$ ; *l*, *m*, *n*, apical drupe and style, apical view,  $\times 1$ ; *o*, *p*, pileus, and style, lateral view,  $\times 1$ ; *q*, apex and style of apical drupe, apical view,  $\times 4$ ; *r*, pileus and style of lateral drupe, distal view,  $\times 4$ ; *s*, style and stigma of lateral drupe, proximal view,  $\times 4$ ; *t*, leaf base, lower side,  $\times 1$ ; *u*, leaf middle, lower side,  $\times 1$ ; *v*, leaf apex, lower side,  $\times 1$ ; *w*, secondary and tertiary veins, lower side, rather near apex,  $\times 4$ .

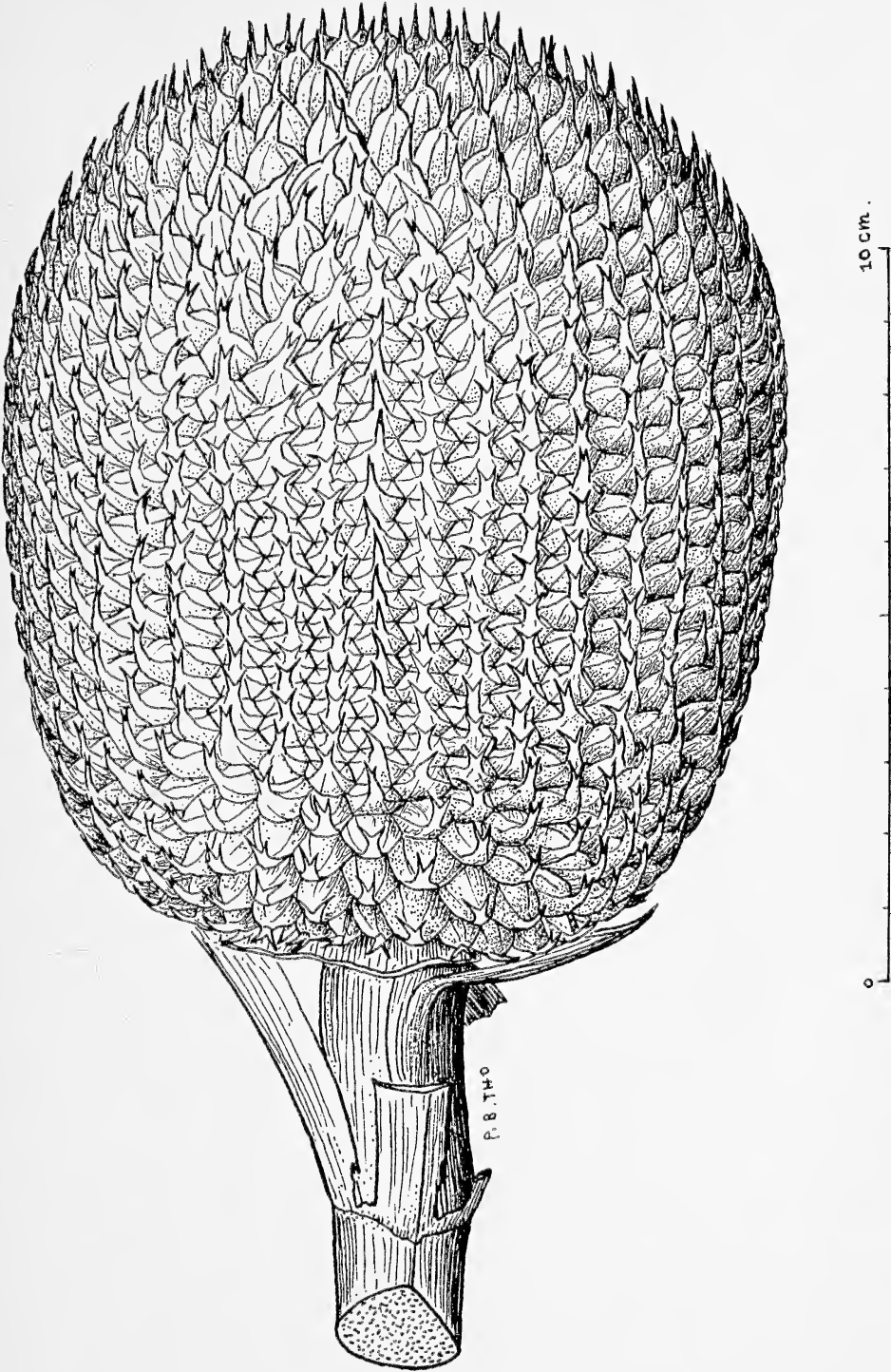


longis adventivis paucis spiniformis adpresse adscendentibus, radicibus fulturosis nullis vel in truncis prostratis 3–5 dm longis 1 cm diametro paucis laevibus vel parve spinosis, foliis 2.73–2.9 m longis 6–6.3 cm latis in media sed proxima basem 5–5.6 cm latis subcoriaceis supra obscure olivaceo-viridibus infra pallide viridibus in basi clausa cupracea supra midnervo late 1-sulcatis 2-plicatis in sectione mediali cum 43 nervis parallelis secundariis in quoque medio in dimidia ultima nervis tertiis conspicuis in lateribus ambis laminis ligulatis sed in basi subcuneatis et in apice subulato trigono gracili breviter diminuentibus eo 10 cm ex apice 1 mm lato basi amplexicauli et inermi sed marginibus ex 10–11 cm cum aculeis 3.5–4 mm longis 11–18 mm separatis subulatis validibus subadscendentibus subviridibus vel albis apicibus brunneis, midnervo infra ex 18 cm cum aculeis 4–5 mm longis 15–25 mm separatis crasse subulatis subreflexis in sectione mediali marginibus cum aculeis 1.5–2.5 mm longis 13–22 mm separatis subulatis adpresse adscendentibus, midnervo infra cum aculeis 3.5–5 mm longis 38–70 mm separatis crasse subulatis reflexis, in apice subulato marginibus et midnervo infra cum serrulis 0.3–0.5 mm longis 1–6 mm separatis, inflorescentia foeminea terminali pendenti cum syncarpio solitario, pedunculo 65 cm longo subclavato in apice 2 cm diametro trigono folioso-bracteato bracteis superis 80 cm longis 7 cm latis, bractea supera 17 cm longa 5.5 cm lata marginibus superis serrulatis, syncarpio cum bracteis marcescentibus subclausis, syncarpio 14 cm longo 12 cm diametro late ellipsoideo valde 3-laterato cum circa 576 drupis eis 33–35 mm longis 9–11 mm latis 7–10 mm crassis oblongo-lanceoloideis 5–7-angulosis (drupis terminalibus parve majoribus et cum stylo subulato arcuato integro) eis lateralibus viridibus subglaucis lateribus planis laevibus parte  $\frac{1}{4}$  supera libera, pileo 12–15 mm alto cum basi 7–10 mm alta 5–7-angulosa oblanceo-pyramidalis lateribus laevibus, stylo 7–8 mm longo cornoso obscure brunneo lucido compresso adscendenti tum valde proxime curvato  $\frac{1}{3}$ – $\frac{2}{5}$  furcato furcis spinosiformibus plerumque divergentibus et subaequalibus, stigmatibus

4–5 mm longo lanceolato bifurcato brunneo papilloso paene ad apices extento, drupis apicalibus cum stylo 5–6 mm longo subulato erecto recto vel subarcuato, endocarpio submediali corpore 14 mm longo osseoso brunneo in apice cum extensioni subulato 8 mm longo lateribus lateralibus 1–1.5 mm crassis intra lucidis, semine 13 mm longo ellipsoideo, mesocarpio apicali cavernoso cum membranis albis medullosis multis, mesocarpio basali parvo fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree, up to 9 m tall, 8 cm in diameter; bark brown, with a few, well spaced, adventive rootlets, up to 1 cm long, appressed ascending, almost spine-like; prop roots none on erect trunks, but on fallen trunks rare and 3–5 dm long, 1 cm in diameter, smooth or with a few remote, small spines; leaves 2.73–2.9 m long, 6–6.3 cm wide at the middle, 5–5.6 cm wide near the base, subcoriaceous, above dark olive green, below pale green, the covered auriculate base copper-colored, broadly furrowed above the midrib, 2-pleated, at midsection with 43 parallel secondary veins in each half, in the outer half the tertiary cross veins conspicuous on both sides, a little sinuous, making a pattern of squares or short oblongs, blade ligulate, though slightly tapering to the base and short tapering to the 10–15 cm, trigonous, slender subulate apex, this 10 cm down 1 mm wide, the base amplexicaul and unarmed, but the margins beginning at 10–11 cm with prickles 3.5–4 mm long, 11–18 mm apart, stout subulate, slightly ascending, greenish to whitish and brown-tipped; the midrib below beginning at 18 cm with prickles 4–5 mm long, 15–25 mm apart, stout subulate, slightly reflexed; at midsection the margins with prickles 1.5–2.5 mm long, 13–22 mm apart, subulate, appressed ascending; the midrib below with prickles 3.5–5 mm long, 38–70 mm apart, stout subulate, reflexed; on the subulate apex the margins and midrib below with serrulations 0.3–0.5 mm long, 1–6 mm apart; pistillate inflorescence terminal, pendent, bearing one syncarp; peduncle 65 cm long, slightly clavate, at apex 2 cm in diameter, trigonous, leafy bracted; upper bracts 80 cm long, 7 cm wide, the innermost 17 cm long, 5.5 cm

FIG. 231. *Pandanus penetrans* St. John, from holotype, syncarp, lateral view,  $\times 1$ .



wide, the upper margins serrulate; syncarp enwrapped and nearly concealed by the marcescent bracts; syncarp 14 cm long, 12 cm in diameter, broad ellipsoid, markedly 3-sided, bearing about 576 drupes, these 33–35 mm long, 9–11 mm wide, 7–10 mm thick, oblong-lanceoloid, 5–7-angled (the apical ones averaging slightly the larger and with a simple, arcuate, subulate style), the normal lateral ones still green, but full sized, a little glaucous, the sides plane and smooth, upper  $\frac{1}{4}$  free; pileus 12–15 mm high, the base oblance-pyramidal, 7–10 mm high, 5–7-angled, the sides smooth; style of lateral and basal drupes 7–8 mm long, horn-like, dark brown, shining, flattened, ascending, then sharply proximally curved almost at right angle, bifurcate  $\frac{1}{3}$ – $\frac{2}{5}$  way, the forks spine-like, mostly divergent and subequal; stigma 4–5 mm long, lanceolate, bifurcate, brown, papillose, extending almost to the tips; apical drupes with simple, subulate style 5–6 mm long, erect, straight or slightly arcuate; endocarp submedian, the body 14 mm long, bony, brown, the apex bearing a subulate prolongation 8 mm long, the lateral walls 1–1.5 mm thick, the inner surface shining; seed 13 mm long, ellipsoid; apical mesocarp a cavern with many white medullary membranes; basal mesocarp scant, fibrous and fleshy.

**HOLOTYPE:** Thailand, Doi Suthet, Chiang Mai, moist forest of *Manglieta Garrattiana* and *Podocarpus nereifolia*, moist stream bank on granite, 1,200 m alt, June 7, 1960, *H. St. John* 26,352 (BISH).

**DISCUSSION:** *P. penetrans* is a member of the section *Rykia*, as is its closest relative, the Malayan species *P. longicaudatus* Holttum & St. John, a species which has the syncarp 16–17 cm long; drupes 41–44 mm long, 8–14 mm wide, cuneate oblong; pileus base 4–6 mm high, pyramidal-hemispheric; stigma 3–3.5 mm long; leaves 4.7–6 cm wide, at midsection with 48 parallel secondary veins in each half, the covered base olive-ochre, and at midsection the midrib unarmed. *P. penetrans* has the syncarp 14 cm long; drupes 33–35 mm long, 9–11 mm wide, oblong-lanceoloid; pileus base 7–10 mm high, oblance-pyramidal; stigma 4–5 mm long; leaves 6–6.3 cm wide, at midsection with 43 parallel secondary veins in each half, the covered base copper-colored, at midsection the midrib below with prickles 3.5–5 mm long, 38–70 mm apart.

The new epithet is the Latin word *penetrans*, penetrating, and is given in reference to the sharp, rigid style forks that easily penetrate one's flesh.

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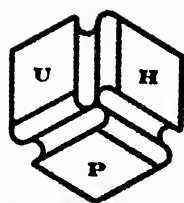
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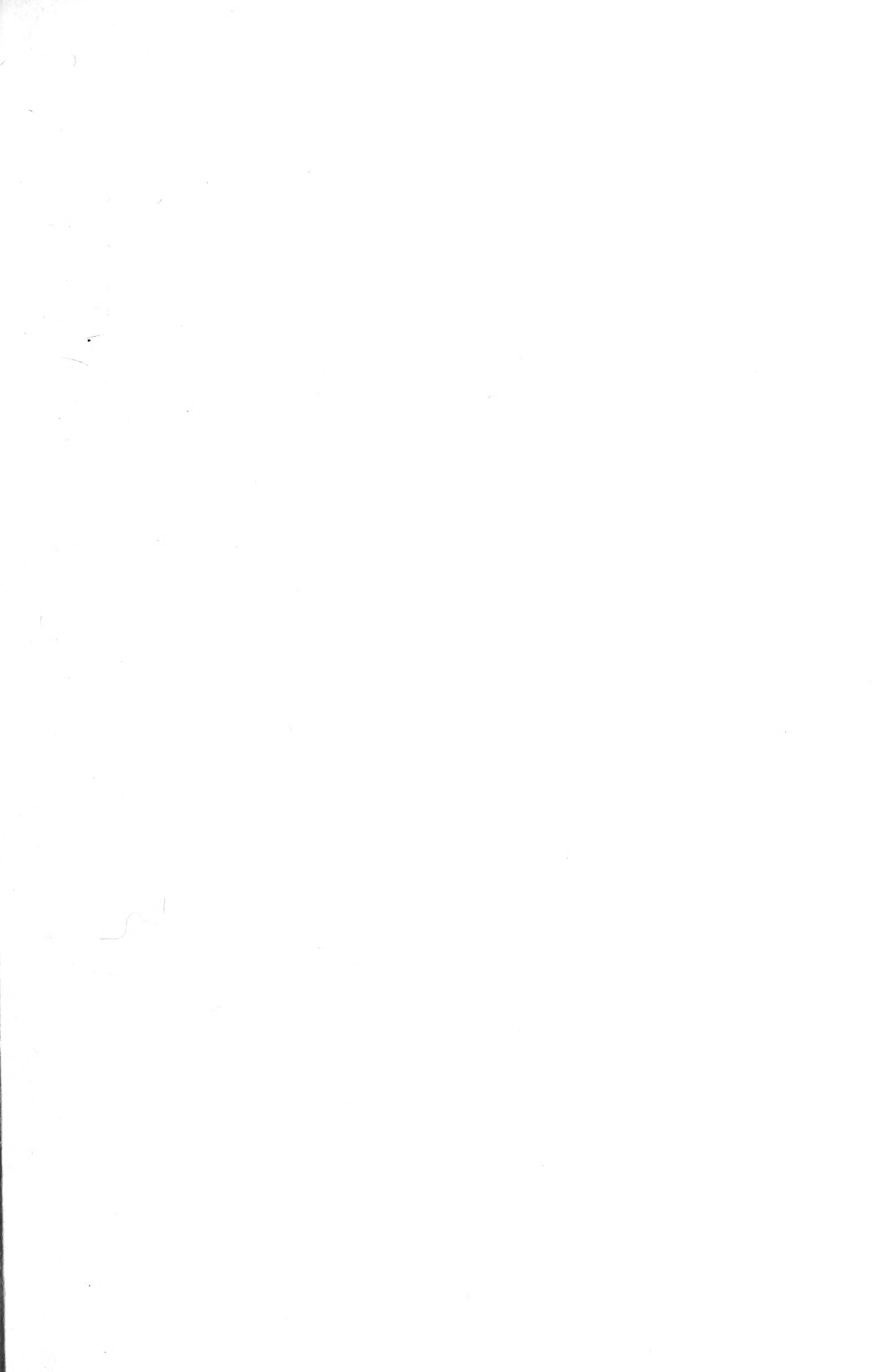
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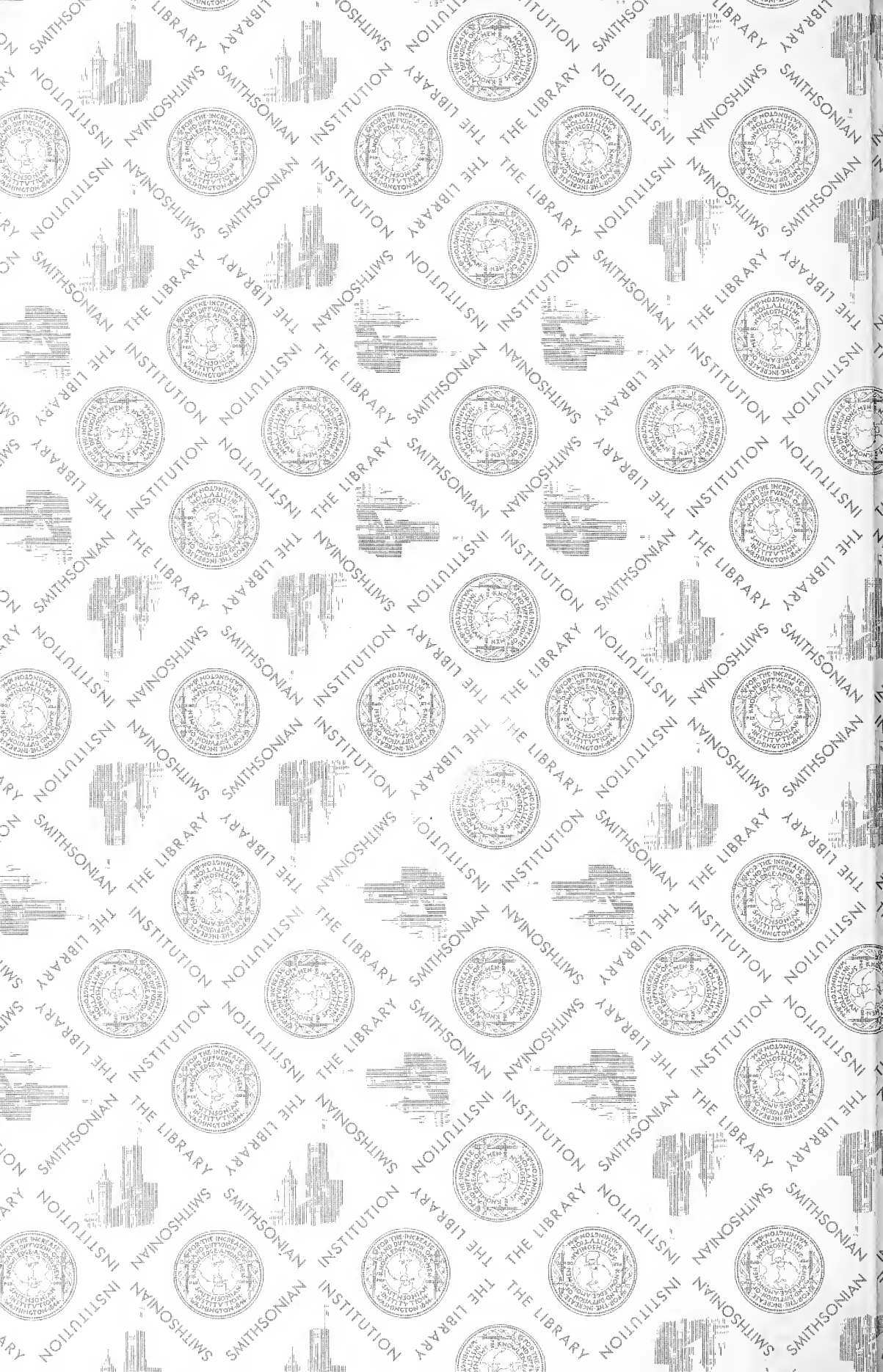


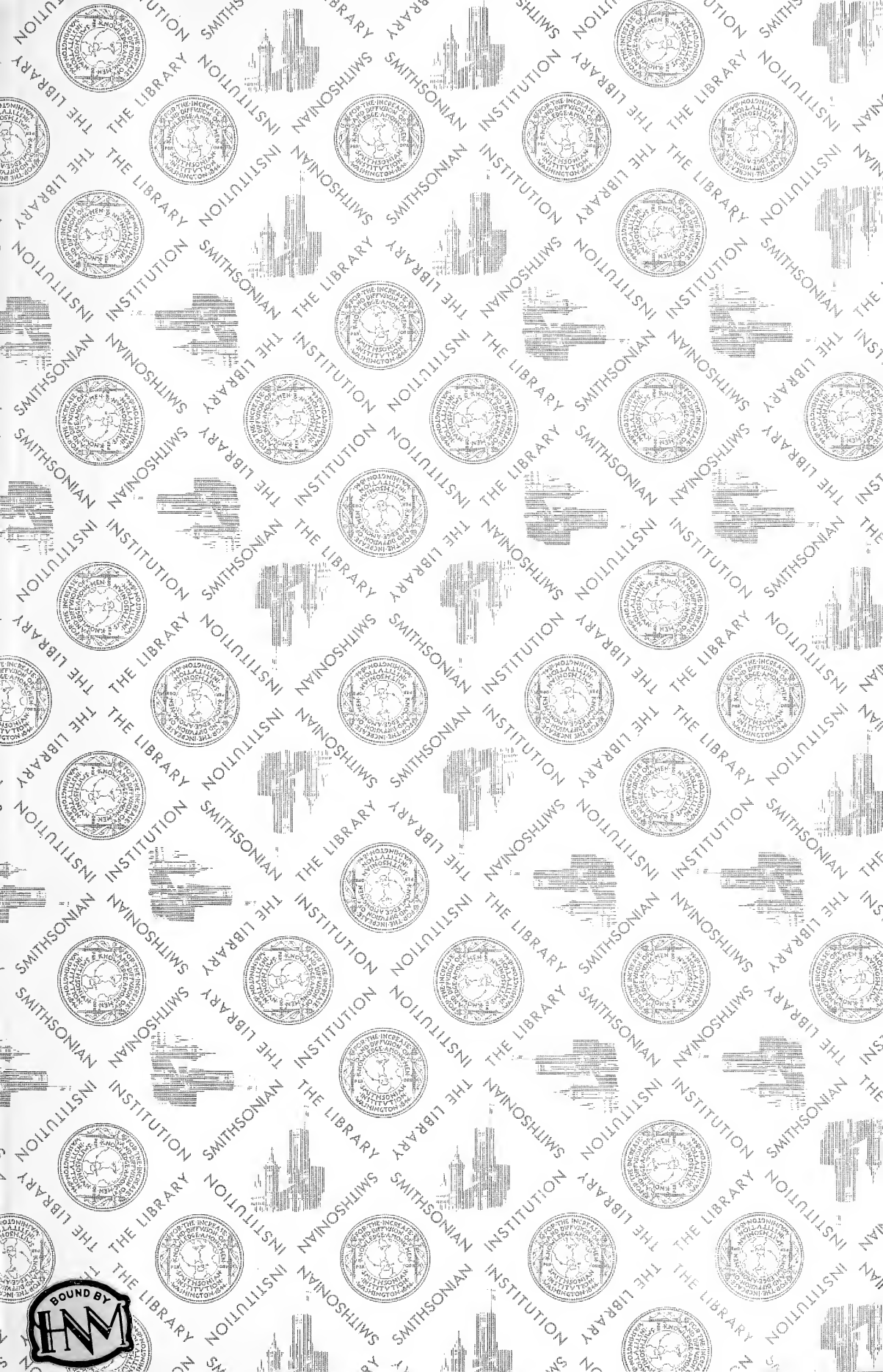












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